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THE SIGNIFICANCE OF CERTAIN NATURAL FLAGELLATES OF INSECTS IN THE EVOLUTION OF DISEASE IN VERTEBRATES

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INTRODUCTION

During the last few years, considerable attention has been given to the rôle of insects in the spread of disease. Much work has been done in elucidating life-histories, more particularly of the parasitic flagellates peculiar to insects and having no apparent connection with vertebrate maladies. Many flagellates that are seemingly limited to insects, however, are not so innocuous to vertebrates as they appear at first sight. The introduction of certain of the parasitic Mastigophora, notably members of the genera *Herpetomonas* and *Crithidia*, into vertebrates by the latter swallowing the infected insects or by forms of the parasite entering the vertebrate host by way of wounds or abrasions of the skin, has been shown to result in pathogenic effects to the said hosts. Laveran and Franchini have demonstrated the existence of this capacity for exercising latent pathogenicity by infecting dogs with the flagellates of dog fleas, and rats and mice with the flagellates of the fleas infesting these rodents. The present authors, working quite independently of Laveran and Franchini, have conducted a series of experiments extending over some six years on the possible pathogenic effects that accrue when certain flagellates of insects reach either associated or unassociated hosts. We have considered more especially the evolution of disease as exemplified by flagellates that have induced a flagellosis in vertebrates, remembering that, at any rate in some cases, parallel conditions prevail in Nature and in our experiments. By the introduction of certain herpetomonads normally parasitic in insects into vertebrates, a condition resembling leishmaniasis or kala-azar in man

has been produced, the symptoms of the disease and the morphology of the parasites found therein showing that here are, at least, examples of "leishmaniasis in the making."

The evolution of the parasitic habit with the development of pathogenicity as the result of change of habitat is no new phenomenon to those who have carefully studied the comparative morphology and life histories of various pathogenic Protozoa. Change of habitat has frequently led to great alteration in the mode of life of an organism. Thus, when a herpetomonad has so adapted itself that it is capable of living and propagating in a vertebrate, as has probably happened in the case of *Leishmania*, an originally monogenetic parasite by the exertion of its capacity for plasticity becomes digenetic. The various herpetomoniasis, of which the leishmaniasis are a special section, are probably the result of the introduction of insect or other invertebrate flagellates into the vertebrate hosts. In the case of acute forms of disease, the excitants show less perfect power of adaptation to the new environment than do the parasites that induce the chronic type of malady. From the point of view of the parasite, the maintenance of the life of the host is an economic desideratum, the prolongation of the active life of the invader depending in part on the longevity of the host. The newer a parasite is to the animal harboring it, the less it is in harmony with its environment. The consequence is that its discord with the host is manifested by pathogenic effects and the latter animal succumbs. Chronic maladies are usually correlated with greater powers of adaptation of the parasite to its host, with the period that has elapsed since the original introduction of the parasite to the host, and with the relative resisting powers of the host to the specific action of the parasite.

Certain trypanosomes appear to have developed from the flagellates of certain insects (for example *Drosophila*), which parasites in turn seem to have been derived from free-living forms. As free-living organisms, their power for harm appears to be negative. If they become saprophytic, their capacity for developing noxious qualities is increased. When the parasitic habit of life, such as bloodsucking, is established in an insect, the power for injury possessed by its contained flagellates is greatly extended. Finally when the insect flagellate reaches the higher vertebrate the recapitulative effects of its evolution manifest themselves with cumulative results and the parasite is definitely pathogenic. The scale of evolution thus outlined is exhibited by the Trypanosomidae, some of whose members, the trypanosomes and herpetomonads (*Leishmania*) of vertebrates are notably pathogenic. While they are in the insect host, to which they have adapted themselves, they are relatively innocuous.

Yet other Protozoa afford studies in the evolution of pathogenicity. It must suffice to mention the case of the malarial parasites. The

morphology of these organisms shows that they are closely allied to the Coccidia, and there is little doubt that the malaria excitants were originally Coccidia of insects, that with change of habitat developed increased powers of adaptation to life in vertebrates, and, at the same time, increased in pathogenicity towards the new host.

The evolution of disease in the past is presented to us by the example of the malarial parasites. Disease in the making is manifested to mankind today in the case of the herpetomonads more especially. Preventive measures gain in efficacy as the natural modes of infection and possible sources of disease excitants are considered. In this connection, the experiments that we have undertaken may be of service as indicating possible sources of disease hitherto unsuspected.

MATERIAL AND METHODS

The materials used in this research consisted of various flagellates found in insects on the one hand, and of representatives of each of the great phyla of European vertebrates on the other.

The flagellates used in our experiments included members of the genera *Herpetomonas* and *Crithidia*. They comprised *Herpetomonas jaculum* Léger, parasitic in the gut of the Hemipteran, *Nepa cinerea*; *H. stratiomyiae* Fanham and Porter, from the intestine of the Dipteran, *Stratiomyia chameleon*; *H. pediculi* Fanham, from the alimentary tract of *Pediculus vestimenti*; *H. culicis* Novy and MacNeal, from the larvae and adults of the gnat, *Culex pipiens*; and *Crithidia gerridis* Patton, parasitic normally in the alimentary tract of the Hemipteran, *Gerris paludum*.

The vertebrate hosts included representatives of the Pisces (*Gasterosteus aculeatus*), Amphibia (*Rana temporaria*, *Bufo vulgaris* and *Molge vulgaris*), Reptilia (*Lacerta vivipara* and *Tropidonotus natrix*), Aves (*Serinus canarius*, *Passer domesticus* and *Chelidon urbica*) and Mammalia (*Canis familiaris* and *Mus musculus*).

The insect flagellates were introduced into their respective vertebrate hosts either by inoculation or by feeding. In the latter case, the host was fed with the infected insects, or with the intestines of the insects, or with food contaminated with the feces of the insects containing the resistant (nonflagellate or postflagellate) stages of the Flagellata concerned. After the infective feed or feeds, ordinary food was given. The hosts were examined for blood parasites and for ectoparasites prior to use, and were found free from both classes of infestation.

Blood films were made periodically during the life of the infected animals, and smears of the internal organs were prepared at autopsy. Some preparations were fixed while moist with osmic vapor followed by absolute alcohol, while others were fixed wet with Bouin's fluid.

Intravital staining was often employed. For permanent preparations Giemsa's stain, hematoxylin and eosin, iron hematoxylin and occasionally hematein were employed.

Control vertebrates were kept in each case. They remained healthy, lived longer than the experimental animals and were found to be unparasitized when killed.

EXPERIMENTAL WORK

The course of our experiments, extending over some years, on the introduction of insect flagellates into vertebrates may be gathered from the subjoined table. It has not been possible to manage a large number of animals satisfactorily at one time, as some have lived for relatively long periods. Sometimes it was possible to introduce the more resistant, encysted, leishmaniform, postflagellate forms of the *Herpetomonas* or *Crithidia* into the vertebrate. In such cases, it was found that a larger proportion of infections ensued than when the preflagellate or flagellate forms alone were introduced.

It is of some interest to note that as a rule the *Herpetomonas* or *Crithidia* introduced were few in number. The parasites, however, adapted themselves to their new surroundings, and both nonflagellate and flagellate organisms in all stages of active division have been recovered from the infected hosts. In some cases it has been possible to observe the completion of the multiplication in fresh preparations of the organs of the host. The parasites in the vertebrates are not merely conserved. The number of parasites obtained from the vertebrate host is superior to that introduced, multiplication of the organisms occurs and the host often undergoes pathogenic changes resembling those of leishmaniasis, that have frequently resulted in death. The herpetomoniasis induced is therefore regarded as a true parasitic infection, both the causal parasites and the maladies having affinities with kala-azar.

The possibility of bacterial contamination of the material used for feeding or inoculation has not been overlooked. Heavy bacterial contamination was exceptional in the insects used for experiment, and here, as elsewhere, the flagellates often die out in the presence of many bacteria. Further, in Nature pure cultures of flagellates or other protozoa rarely occur, as, for example, is evidenced by the diverse organisms found in sores of man in the East and in the mixed flora and fauna of the alimentary tract of vertebrates. Also, the insects swallowed by such vertebrates as lizards and snakes cannot, of necessity, contain pure cultures of flagellates or bacteria—in fact, mixed infections are frequent in Nature.

The tabular summary of our experiments is given on page 154.

From the following table, it will be seen that while a number of the infections are of the acute type, yet there are others in which the herpetomoniasis induced was of relatively long duration. We may mention that when the infection was of the chronic type, the leishmaniform, nonflagellate bodies preponderated in the smears of the organs of the vertebrate host, while flagellate herpetomonads were more numerous in the cases of acute herpetomoniasis. In practically all the animals infected experimentally, both nonflagellate and flagellate forms of the organism introduced were present, the proportion of each form showing variation. While these conditions prevailed in our experiments, we do not consider that any generalization can yet be made therefrom.

We would also point out that our experiments show the potential danger of many flagellates of insects that may at first sight seem unconnected with the vertebrates into which they have been introduced. Natural modes of infection, however, occur with a number of examples; thus, the dog may contract infection with herpetomonads by eating dog fleas and by ingesting infected flea feces when licking its coat, *H. jaculum* from *Nepa cinerea* can easily reach the fish and amphibia which it attacks and may even reach man by way of the wounds inflicted by the raptorial cutting forelimbs used when the insect sucks blood. The case of insectivorous birds whose normal food is insects is obvious. The experiments, whether between associated or unassociated insect flagellates and vertebrates, show "leishmaniasis in the making."

The chronic infections afford examples of good powers of adaptation to environment on the part of the parasites. As noted in our introduction, it is to the advantage of the newly established organism that the life of the host should be prolonged, and thus the continued existence of the parasite ensured. The acute cases are marked by the rapid development of the flagellate forms of the organisms, and by their less perfect adaptation to new surroundings as manifested in their pathogenic effects to their new hosts.

A further point of interest is that when young hosts were used, the parasites were more virulent. This is also the case with the parasites causing the human disease, Mediterranean kala-azar, which is prevalent more especially in children.

MORPHOLOGY OF THE PARASITES IN THE VERTEBRATE AND INVERTEBRATE HOSTS

The life-history of a herpetomonad in its insect host may be briefly outlined as follows: A *Herpetomonas* is a flagellate possessing also a nonflagellate stage in its life-cycle. This nonflagellate form is an ovoid or rounded, leishmania-like body containing a nucleus and a blepharoplast. It (Fig. 1a) may be passed from the host with the feces of the

TABLE—RESULTS OF THE EXPERIMENTAL INFECTIONS OF DIFFERENT VERTEBRATES WITH VARIOUS HERPETOMONAS AND CRITHIDIA FROM INSECTS

No. of Experiment	Vertebrate Host	Flagellate Introduced	Mode of Introduction	Duration of Life of Host	Effect on Host	Forms of Parasites Observed in the Vertebrates	Remarks
1	Wild mouse, <i>Mus musculus</i> , ♀	<i>Herpetomonas jaculum</i>	Feeding.....	50 hours.....	Acute herpetomoniasis	Flagellate and non-flagellate	Young host
2	Wild mouse, ♂	<i>Herpetomonas jaculum</i>	Feeding.....	70 hours.....	Acute herpetomoniasis	Flagellate and non-flagellate	Young host
3	Wild mouse, ♀	<i>Herpetomonas jaculum</i>	Intraperitoneal inoculation	60 hours.....	Acute herpetomoniasis	Flagellate and non-flagellate	Young host
4	Wild mouse, ♂	<i>Herpetomonas jaculum</i>	Feeding.....	60 hours.....	Acute herpetomoniasis	Flagellate and non-flagellate	Host killed in extremis
5	Wild mouse, ♀	<i>Herpetomonas jaculum</i>	Feeding.....	84 hours.....	Acute herpetomoniasis	Flagellate and non-flagellate	Host killed when very ill
6	Wild mouse, ♂	<i>Herpetomonas jaculum</i>	Intraperitoneal inoculation	72 hours.....	Acute herpetomoniasis	Flagellate and non-flagellate	Host killed in extremis
7	Adult mouse, ♂	<i>Herpetomonas jaculum</i>	Intraperitoneal inoculation	Killed after 8 months	No symptoms of disease	Few non-flagellate.	Spontaneous cure, no parasites found at autopsy
8	Mouse, ♂	<i>Herpetomonas stratiomyiae</i> ..	Feeding.....	5 days.....	Herpetomoniasis induced	Nonflagellate and some immature flagellate	Young host
9	Mouse, ♀, adult.....	<i>Herpetomonas pediculi</i>	Feeding.....	72 days.....	Herpetomoniasis induced	Mostly nonflagellate, very few flagellate forms	Chronic infection
10	Mouse, ♀, adult.....	<i>Herpetomonas pediculi</i>	Fed on liver of No. 9	15 days.....	Herpetomoniasis induced	Non flagellate and flagellate	Killed in extremis.
11	Mouse, ♀, adult.....	<i>Crithidia gerridis</i>	Intraperitoneal inoculation	40 days.....	Infection with <i>C. gerridis</i> induced	Flagellate and non-flagellate forms, the latter more numerous	Skin sore and alopecia at the site of inoculation
12	Mouse, ♀, adult.....	<i>Crithidia gerridis</i>	Subcutaneous inoculation	2 months, then killed	Negative		
13	Mouse, ♂, adult.....	<i>Crithidia gerridis</i>	Feeding.....	38 days.....	Infection with <i>C. gerridis</i> induced	Flagellate and non-flagellate, the latter predominating	Young host. Spontaneous cure. No parasites found when killed
14	Dog, <i>Canis familiaris</i> , ♂	<i>Herpetomonas ctenocephali</i> ..	Feeding.....	Killed after 15 months	No marked permanent ill-effects	Nonflagellate.....	

15	Canary, <i>Serinus canarius</i> , ♀, adult	<i>Herpetomonas jaculum</i>	Feeding.....	51 days.....	Chronic herpetomoniasis induced	Many nonflagellate, a few flagellate	Note chronic infection probably to be correlated with the presence of non-flagellate forms
16	Sparrow, <i>Passer domesticus</i> , ♀, adult	<i>Herpetomonas culicis</i>	Feeding.....	9 days.....	Acute herpetomoniasis induced	Flagellate and non-flagellate, the former predominating	Note acute infection, probably to be correlated with the presence of many flagellate forms
17	Martin, <i>Chelidon urbidia</i> , ♂, young adult	<i>Herpetomonas culicis</i>	Feeding.....	12 days.....	Acute herpetomoniasis induced	Flagellate and non-flagellate, the former dominant	Note acute infection and many flagellate forms present
18	Martin, ♀, young adult	<i>Herpetomonas culicis</i>	Subcutaneous inoculation	2 days.....			Probably died of fright
19	Canary, ♂, young...	<i>Herpetomonas jaculum</i>	Feeding with infected insect excrement	17 days.....	Herpetomoniasis induced	Flagellate and non-flagellate	
20	Martin, ♂, mature young	<i>Herpetomonas culicis</i>	Feeding with infected insect excrement	32 days.....	Herpetomoniasis induced	Nonflagellate and a few flagellate	
21	Sparrow, ♀.....	<i>Herpetomonas jaculum</i>	Feeding with infected insect excrement	Killed after 3 months		One parasite only seen during life	Spontaneous cure. No parasites found at autopsy
22	Canary, ♀, adult....	<i>Herpetomonas culicis</i>	Fed on food contaminated with <i>H. culicis</i>	Killed after 80 days	Negative		
23	Grass snake, <i>Tropidonotus natrix</i> , ♂	<i>Herpetomonas jaculum</i>	Feeding.....	20 days.....	Herpetomoniasis induced	Flagellate and non-flagellate	
24	Lizard, <i>Lacerta vivipara</i> , ♂	<i>Criethidia geridis</i>	Feeding.....	19 days.....	Infection with <i>C. geridis</i> induced	Flagellate and non-flagellate	
25	Lizard, ♂	<i>Criethidia geridis</i>	Fed on infected liver of No. 24	6 days.....	Acute disease (criethidiasis)	Flagellate and non-flagellate	Second passage
26	Lizard, ♀.....	<i>Criethidia geridis</i>	Intraperitoneal inoculation with infected heart blood of No. 24	Killed after 20 days	Slight infection	Nonflagellate	Killed for examination after 20 days. Third passage
27	Frog, <i>Rana temporaria</i> , ♂, adult.....	<i>Criethidia geridis</i>	Intraperitoneal inoculation of No. 25	29 days.....	Infection with <i>C. geridis</i> induced	Flagellate and non-flagellate	
28	Frog, ♂, adult.....	<i>Herpetomonas jaculum</i>	Intraperitoneal inoculation	54 days.....	Herpetomoniasis induced	Flagellate and non-flagellate	
29	Toad, <i>Bufo vulgaris</i> , ♂, adult.....	<i>Herpetomonas jaculum</i>	Subcutaneous inoculation	40 days.....	Chronic infection	Nonflagellate and young flagellate	
30	Toad, ♀, adult.....	<i>Herpetomonas jaculum</i>	Intraperitoneal inoculation	80 days.....	Negative	None	
31	Newt, <i>Molge vulgaris</i> , ♂, young adult	<i>Herpetomonas jaculum</i>	Feeding.....	9 days.....	Apparently negative	None	Death by misadventure
32	Stickleback, <i>Gasterosteus aculeatus</i> , ♂	<i>Herpetomonas jaculum</i>	Feeding.....	2 days.....		None	
33	Stickleback, ♂.....	<i>Herpetomonas jaculum</i>	Subcutaneous inoculation	6 days.....	Herpetomoniasis induced	Flagellate and non-flagellate	

latter, and is then surrounded with an outer coat. If the excrement containing the nonflagellate—sometimes termed encysted or postflagellate—forms of the herpetomonad is ingested by another insect host, these ovoid forms of the parasite have their firm, varnish-like outer coat (Fig. 1f) dissolved by the digestive juices of the host and are then capable of further development. In this condition, they are often termed preflagellate forms (Fig. 1a). The preflagellate form gradually elongates. A flagellum arises near the blepharoplast (Fig. 1c), reaches the surface of the body at the anterior end and finally projects as a free flagellum. The posterior end also elongates and thus the typical flagellate is produced (Fig. 1d).

Multiplication of the flagellate by longitudinal division can occur in either the nonflagellate (Fig. 1b) or the flagellate stage (Fig. 1e). As the organisms pass onward into the less favorable environment of

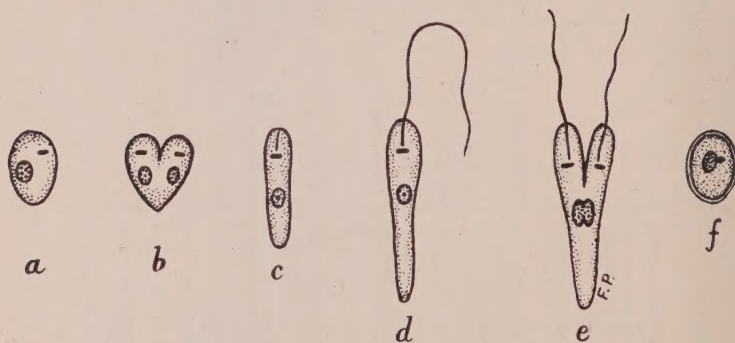


Fig. 1.—*Herpetomonas*: (a) non-flagellate or leishmaniform stage; (b) dividing non-flagellate; (c) elongating parasite; (d) flagellate stage; (e) dividing flagellate; (f) post-flagellate or encysted stage. $\times 1500$.

the posterior end of the intestine of their host, their body cytoplasm concentrates, and the flagellum is withdrawn and largely dissolved. The now ovoid parasite secretes a coat which may be at first gelatinous but ultimately becomes varnish-like or "skin tight" and the postflagellate form is again produced. This resistant nonflagellate form (Fig. 1f) is particularly adapted for extracorporeal life and serves for the safe transference of the parasite from host to host.

The above outline of the life history of a herpetomonad is valid for *Herpetomonas jaculum*, *H. stratiomyiae*, *H. pediculi*, *H. culicis* and *H. ctenocephali* with which we experimented.

The life-history of a true *Crithidia*, such as *C. gerridis*, in its insect host has the same general outline as that of a *Herpetomonas*. But the flagellate stage differs from that of a *Herpetomonas* in that at the differentiation of a flagellum, this structure not only reaches the sur-

face, but forces the ectoplasm before it, thus producing a small wavy undulating membrane that gradually fades into the free flagellum at the tapering anterior, flagellar end of the body of the organism (Fig. 2b).

The morphology of *Herpetomonas jaculum*, *H. stratiomyiae*, *H. pediculi*, *H. culicis* and *H. ctenocephali* in the vertebrate hosts into which they were introduced resembled that in the invertebrate hosts. The parasites have been introduced both as flagellates and as nonflagellates. In blood smears taken during the life of the host and in organ smears made at autopsy, usually both flagellate and nonflagellate forms were found. Parasites in various stages of multiplication were

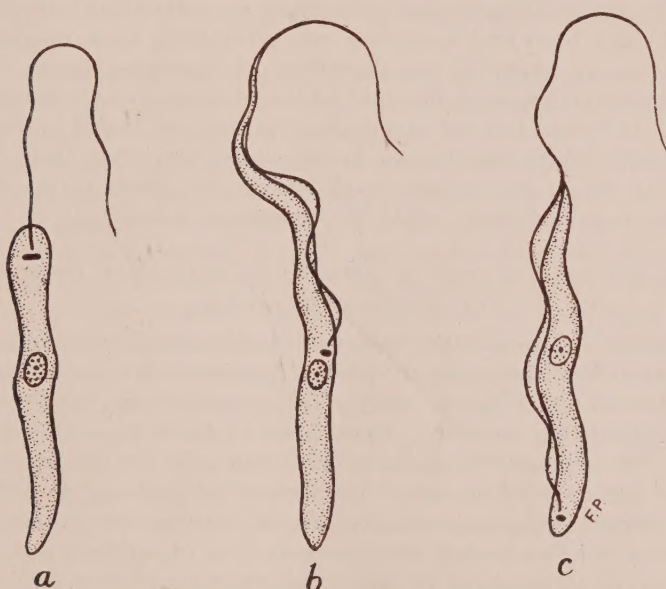


Fig. 2.—Flagellate forms of (a) *Herpetomonas* (sometimes called *Leptomonas*), (b) *Crithidia* and (c) *Trypanosoma*. $\times 2000$.

observed in the fresh condition and in stained preparations. Hence there is definite evidence that they had become true parasites of the vertebrates, had established themselves and had increased in numbers in them, and were not mere conservations of the forms introduced.

The various *Herpetomonas* (Fig. 2a) and *Crithidia* (Fig. 2b) that we have used have retained the facies that they presented in the insect hosts. No transition to a trypanosome (Fig. 2c) was ever seen by us during the course of these experiments. The only variation presented by the parasites in the vertebrates from that in the invertebrates was that the maximum length of the insectan flagellate stage was not usually quite attained. The sizes of the parasites, however, were

always well within the range of the limits of variation given for the insect parasites and were of good average size. Morphologically, they were replicas of the insect forms and could be unmistakably identified with them. The nonflagellate forms were about the size of or slightly greater than the Leishman-Donovan body in man, while the dimensions of the flagellate forms were much the same as those of *Leishmania* in cultures on the Novy-MacNeal-Nicolle medium, that is, about 15μ to 20μ in the long diameter of body. The slightly lesser dimensions of the parasites may be the results of transference and implanting of the organisms in new hosts, or perhaps the age of the host may influence the size of the parasite. It has been noticed that other parasites, for instance, certain *Haemosporidia*, introduced into unfamiliar vertebrates or into young hosts tend to produce new generations whose maximum dimensions are somewhat less than those of their progenitors. The same factors may apply in this induced herpetomoniasis. On the other hand, it is known that the nonflagellate parasite of Indian kala-azar maintained in dogs may increase in longest diameter from about 2.5μ or 3.5μ to 8μ or 9μ . Similar variations in size occur in the non-flagellate stages of closely allied herpetomonads in insects.

THE SIGNIFICANCE OF CERTAIN NATURAL FLAGELLATES OF INSECTS IN
THE EVOLUTION OF DISEASE

The rôle of insects in the spread of disease among men and other animals has furnished some of the most important advances in knowledge made in recent times. Many parasitic protozoa are the descendants of free-living ancestors. The degrees of degradation from independent life to saprophytism and thence to parasitism are almost imperceptible but nevertheless exist. Neither are the grades of parasitism more well defined, and consequently a free-living organism that by accident or chance has reached the alimentary tract of an insect may live there first as a saprophyte, feeding on the waste materials or the newly ingested food of the host. The minute quantities of nourishment lost by the host in this way become serious when cumulative, and the saprophytism then leads to parasitism of a somewhat low degree. When the living protoplasm of the host furnishes the nutriment required, the parasitism becomes obvious and the effects on the host are more or less marked.

In the case of many intestinal flagellates of insects, the host has responded to the attacks of the parasites in such a way that a mutual toleration has become established between them. Under these circumstances but little injury ensues to the host, and the flagellates concerned are considered as "natural" and practically harmless to the host. Further, they have often been considered as specific to the said hosts to which they are practically harmless.

Should such flagellates reach a vertebrate host, two courses may result. In the first instance, the flagellates may merely perish. In the second case, should the introduced organism be sufficiently plastic, it may adapt itself to its new environment and be able to persist for a time. Should its powers of adaptation be marked, it will multiply, and the greater the rapidity of increase, the greater the danger to the host. In other words, environment and plasticity determine pathogenicity.

Certain of the flagellates show the transformation from almost harmlessness in the insect to pathogenicity in the vertebrate or newer host. The genus *Herpetomonas* affords a good example of the capacity for pathogenicity that may be latent in many organisms hitherto considered harmless.

Kala-azar, oriental sore and dermumucosal leishmaniasis are well-known tropical diseases due to members of the *Herpetomonadidae* that are known as *Leishmania donovani*, and *L. infantum* in the cases of kala-azar, and as *L. tropica* in the more local maladies of the skin. These organisms are, in all probability, herpetomonads of insects that have reached vertebrate hosts. It is known that the various species of *Leishmania* develop into typical herpetomonad flagellates in cultures, and for some time now these flagellate stages have been known in man. Thus, in 1911, Escomel saw flagellate forms of *Leishmania tropica* in man and published about them later. La Cava in 1912 described similar forms of the same parasite in Italy. Also in 1912, Splendore found elongating forms and a few flagellate parasites in dermumucosal leishmaniasis in Brazil, while Monge in 1914, when working on the same malady in Peru, found the herpetomonad stage of the parasite. Lately (September, 1915) Wenyon has found the flagellate stage of *Leishmania donovani* in a dog subinoculated from other dogs, the strain being originally derived from a man who died of kala-azar contracted in Calcutta. Further, a new herpetomonad, *Haemocystozoon brasiliense*, was found by Franchini in 1913 in a human subject.

As a result of experimental work, such as that of Patton and of Wenyon, it has been shown that species of *Leishmania* can develop into herpetomonad flagellate stages within the intestines of certain insects, such as bedbugs and mosquitos (*Stegomyia*). The evidence that an ovoid *Leishmania* is the non-flagellate stage of a herpetomonas is proved, and the flagellate stage of *Leishmania* can exist in cultures, in insects and in man. *Leishmania* morphologically is a herpetomonad.

Herpetomonads experimentally introduced into vertebrates by us have produced pathogenic effects recalling those of kala-azar. Both maladies present the same features—the insidious onset, the subsequent relatively rapid illness, the splenic and often hepatic enlargement, feverish attacks and emaciation. In the cases where chronic infections

were produced in our animals, the nonflagellate, leishmaniform stages of the parasites were more numerous, while in acute cases the flagellate forms were more obvious (see table). In the diseases due to *Leishmania* spp. the flagellate forms in the vertebrate host are far less common than the nonflagellate ones, but it is of distinct interest to note that Monge (1914) suggested that the presence of flagellate forms of *L. tropica* in man was an indication of increased virulence on the part of the parasite. Such an increased virulence certainly coincided with more marked development of flagellates in our animals. Though no general conclusion on the subject can yet be given, the hypothesis that the presence of flagellate *Herpetomonas* or *Leishmania* in the vertebrate host affords an index of virulence is supported by the experimental results that we have obtained.

The part played by vertebrates proved capable of harboring herpetomonads is one that demands the attention of all students of preventive medicine and of sanitary reform. By experiment we have proved that flagellates belonging to the genera *Herpetomonas* and *Criethidia* have produced infections not only in mammalia like mice and dogs, but also in birds and in cold-blooded vertebrates such as members of the pisces, amphibia and reptilia. Further, these flagellates are capable of assuming resting, nonflagellate stages in these hosts.

There is thus the possibility that various vertebrates—fish, amphibia, birds, reptilia, and mammals—may serve as reservoirs of the herpetomoniasis, including leishmaniasis. The virus may be very attenuated and so escape detection, or only be revealed by the presence of flagellate forms in cultures. Recently (1914) Sergeant, Lemaire and Senevet in Algeria have demonstrated the presence of a herpetomonad flagellate in the blood and organs of geckos obtained from areas in Algeria in which oriental sore due to *L. tropica* is present. *Phlebotomus* flies, which may harbor a natural herpetomonad, feed on the geckos and on man. Hence animals like geckos may possibly act as reservoirs of leishmaniasis. Chatton and Blanc (1914) have found possible leishmaniform bodies in the young red blood cells of geckos in Tunis. Bayon (1915) has found herpetomonad parasites in the cloaca of *Chameleon pumilus* at Robben Island, South Africa, and says that "it does not seem excluded that a chameleon can get infected through swallowing a fly containing *Herpetomonidae* in its gut." He also found a herpetomonad in the gut of the fly, *Scatophaga hottentota*, in the same place. Lindsay (1914) stated that the parasite of dermofucosal leishmaniasis in Paraguay is believed by native sufferers to be conserved in rattlesnakes and to be spread by ticks or flies (*Simulium*) feeding on the reptiles and transferring the parasite to man. We have shown the possibility of such infection occurring by causing insectivorous vertebrates, such as viviparous lizards and grass snakes, to

ingest insects infected with herpetomonads, wherewith the vertebrates became parasitised. Similarly, insectivorous birds have become parasitised by ingesting insects containing herpetomonads. These infections could be accomplished in Nature and, in fact, such parasitism of a bird by herpetomonads and of mice by the same flagellates has been found (see below). Natural reservoirs of herpetomoniasis, consisting of vertebrates on which sanguivorous insects feed, should be sought for in areas where diseases such as kala-azar are present.

Natural reservoirs of herpetomoniasis are already known. Man and his intimate domestic associate the dog, both may function as reservoirs of what has been termed Mediterranean or infantile kala-azar. The parasite, *Leishmania infantum*, which is often considered to be a form of *L. donovani*, is thought to be transmitted from dog to dog by the dog flea and possibly also from dog to man. An infected child or an infected dog may, perhaps, serve as the reservoir of the virus. In this connection it is of some interest to recall that cattle which have become immune to piroplasmosis may yet harbor sufficient sparse piroplasms in their blood to infect many ticks and so spread the malady. Analogy is somewhat dangerous, but in this case, it may be of service, since rare cases of "spontaneous cure" of infantile leishmaniasis are known and it is just possible that such may act as unsuspected reservoirs of leishmaniasis.

Vertebrates other than man can be infected naturally with herpetomonads. In 1903, Dutton and Todd described herpetomonads from the blood of house mice in Senegambia. The original description was very definitely that of a *Herpetomonas*, though Todd has recently stated that he thinks the organism may have been a trypanosome. However, we have also found herpetomonads closely resembling those described by Dutton and Todd in mice in England. It is known that the common rat-fleas contain herpetomonads and it is suggested that these fleas were the probable source of infection. Mice as possible reservoirs of leishmaniasis cannot be disregarded.

Again, a natural infection of birds has been described by Drs. Edmond and Etienne Sergent. In this case a pigeon was found to contain herpetomonads in its blood. The source of the flagellate is not known with certainty, but we advance the hypothesis that it was a latent herpetomoniasis contracted from herpetomonad-infected insects such as species of *Lynchia* that had fed on the bird.

From a careful comparison of natural and induced herpetomoniasis in vertebrates and of leishmaniasis, as well as consideration of the morphology and life phenomena of the excitants in each case, the following general statements can be made. Under suitable conditions, insect flagellates can be introduced into vertebrate hosts and can produce infections therein. In some cases, as in some cold-blooded verte-

brates, little obvious ill effect results; in others, as in mammals and birds, disease is manifested and often ends in death.

The organisms, such as herpetomonads, thus introduced, retain their powers of development on the same lines as when they were present in the insects. The morphological cycle is that of *Herpetomonas*. The various species of *Leishmania* are probably insect flagellates long since introduced into man and usually perpetuating the nonflagellate form, though capable of assuming the flagellate, herpetomonad facies in the internal organs of the vertebrate or in the invertebrate hosts.

No insect flagellate can be considered to be quite innocuous to vertebrates until it has been put to the test.

It must be remembered that leishmaniasis, which is a form of herpetomoniasis, is a flagellosis, as is also trypanosomiasis. The treatment of leishmaniasis by intravenous injection of tartar emetic—as advocated and practiced recently—is sound biologically, for drugs containing arsenic or antimony have proved efficacious in trypanosomiasis.

It is necessary to consider not part, but the whole, of the life history of an organism and also the relationship of the parasite to the group to which it belongs. There is a line of evolution common to each group and in these cases, neither *Herpetomonas* (*Leptomonas*), *Leishmania*, *Crithidia* nor *Trypanosoma* (Fig. 2) should be considered as isolated units but as flagellates belonging to the *Trypanosomidae*.

MODES OF INFECTION AND PREVENTIVE MEASURES AGAINST ARTHROPOD-BORNE HERPETOMONIASIS

The experiments on the introduction of various species of *Herpetomonas* and *Crithidia* parasitic in insects into both warm and cold-blooded susceptible vertebrates has shown that these flagellates can produce an infection in the vertebrates when the latter are fed or inoculated with them. Within the host, the parasite is capable of assuming the leishmaniform or flagellate facies. The mode of infection of the vertebrate in nature seems to be contaminative, either by its food, or through an already existing abrasion or puncture on the surface of its body. The feces of insects, if containing the resistant forms of the flagellate, are capable of producing infection by similar channels. We have also obtained evidence showing that postflagellate forms of the parasite are the best adapted to begin life in a new vertebrate host.

Experiments on ourselves with fleas and lice, and with biting insects on rats, suggest that infection with *Herpetomonas* or *Leishmania* is not by inoculation with the protozoal parasites during the time when the insect is biting man or other vertebrate, but by the vertebrate eating the infected insect, or by infected insect feces passing through an abrasion, puncture or bite on the vertebrate skin. In this connection it is of

interest to note that Laveran has quite recently succeeded in infecting a mouse with a culture of *Leishmania tropica* by way of the mouth.

As we have already stated, in areas where leishmaniasis are endemic, an examination should be made of all insects and other invertebrates likely to come into contact with men or dogs or rats and mice, in order to ascertain if these invertebrates harbor herpetomonads. Preventive measures should be directed against such invertebrates, especially arthropods. Further, it is likely that certain vertebrates, such as reptiles and amphibia (especially such as are insectivorous), may serve as reservoirs for leishmaniasis or, as they should preferably be termed, herpetomoniasis. From such reservoirs the herpetomonads may reach man by the agency of ectoparasites or flies, especially such as are sanguivorous.

That some of these suggestions are of practical application has been proved by the work of Dodds Price in the Assam tea gardens, following on a suggestion from Rogers to the effect that action should be taken against suspected transmitters of kala-azar, even if complete incultation of them had not been afforded. Dodds Price has reduced the mortality due to kala-azar enormously by segregating the infected, by moving coolie lines about three hundred yards from older, infected ones and by having new coolie lines placed on clean sites. Young (1914) has applied successful segregation measures to an indigenous population in certain villages in Assam. These measures check the prevalence of sanguivorous insects that infest man and his dwellings, and reduce the danger of possible infection by way of contaminated food or drink. It may be expected that the application of similar measures in other areas where kala-azar is endemic may also be equally efficacious.

SUMMARY

1. Herpetomoniasis can be induced in various warm and cold-blooded vertebrates when the latter are inoculated or fed with herpetomonads occurring in the digestive tracts of various insects. The infection produced and the protozoal parasites found in the vertebrates resemble those of human and canine leishmaniasis.

2. An infection can also be induced in certain vertebrates when they are fed or inoculated with *Crithidia gerridis*, and both flagellate and nonflagellate stages occur therein, but no transition to a trypanosome was found.

3. The following Flagellata have been proved pathogenic to warm-blooded vertebrates when the latter have been fed, or inoculated subcutaneously or intraperitoneally with them—*Herpetomonas jaculum*, *H. stratiomyiae*, *H. pediculi*, *H. ctenocephali*, *H. culicis* and *Crithidia gerridis*. The hosts used were mice of various ages, dogs, canaries, sparrows and martins.

4. *Herpetomonas jaculum* and *Crithidia gerridis* have also been successfully fed or inoculated into cold-blooded hosts, namely, fishes (*Gasterosteus aculeatus*), frogs, toads, lizards (*Lacerta vivipara*) and grass-snakes (*Tropidonotus natrix*).

5. The disease induced may run an acute or a chronic course. In the acute cases among our vertebrates the flagellate form of the parasite was the more obvious at death. In chronic cases, non-flagellate forms of the parasite were more numerous.

6. Natural herpetomoniasis of a pigeon has been recorded by Drs. Edm. and Et. Sergent in Algeria. This affords a parallel case with the natural and induced herpetomoniasis of mice as recorded by us.

7. The flagellate stage of *Leishmania donovani* in vertebrates is now known, and that of *L. tropica* in man has been known for some time. The links completing the evidence that a *Leishmania* is morphologically a *Herpetomonas* are thus complete. We believe that leishmaniasis are invertebrate-borne herpetomoniasis, and that these maladies have been evolved from flagellates of invertebrates (especially herpetomonads of insects), which have been able to adapt themselves to life in vertebrates.

8. In areas where leishmaniasis are endemic an examination should be made of all insects and other invertebrates likely to come into contact with men or dogs or domestic vermin like rats and mice, in order to ascertain if these invertebrates harbor herpetomonads. Preventive measures should be directed against such invertebrates, especially arthropods. Further, it is likely that members of all classes of vertebrates, and especially those members that are insectivorous, may serve as reservoirs for leishmaniasis, or as they should preferably be termed, herpetomoniasis. The virus may exist in such reservoirs in a very attenuated condition and so be difficult of detection. From these sources the herpetomonads may reach man by the agency of ectoparasites or flies, especially such as are sanguivorous.

ADDENDUM

As this paper—the writing of which has been greatly delayed by war work—was on the point of being despatched, our attention was drawn to an article on The Insect Vector of Uta by C. H. T. Townsend in the December number of the *Journal of Parasitology*, just received in England. The concluding paragraph of the text and more particularly of the summary of Townsend's paper were read by us with very great interest, as they confirm our conclusions regarding leishmaniasis being arthropod-borne herpetomoniasis. This conclusion of ours has met with considerable opposition at the hands of Wenyon, much to our

surprise, and in spite of the fact that the experiments of Laveran and Franchini, as well as the much more extended series of our own, admit of no other conclusion to our mind.

The following conclusions of ours may be compared with those of Townsend (December, 1915). Thus, in November, 1914, we stated that, "It may be expected that the various leishmaniasis, occurring in different parts of the world, will prove to be insect-borne herpetomoniasis." Again, in May, 1915, we wrote that: "As we have previously stated, we believe that leishmaniasis are arthropod-borne herpetomoniasis, and that these maladies have been evolved from flagellates of invertebrates (especially herpetomonads of insects), which have been able to adapt themselves to life in vertebrates." Further, one of us in June, 1915, wrote that: "It is inferred that the various leishmaniasis are due to a herpetomonad of invertebrates which, under different conditions of environment, produces pathogenic effects in very varying degrees in different vertebrates, from zero, as in the mice described by Dutton and Todd in 1903, to high mortality as in Indian kala-azar, and probably zero again in cold-blooded hosts. It is also a flagellate which can probably live in invertebrates not already recorded as being infected. A human reservoir of leishmaniasis may occur in some places, while warm and cold-blooded vertebrates may also function as the same."

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A REVISION OF THE GENUS ARHYTHMORHYNCHUS

WITH DESCRIPTIONS OF TWO NEW SPECIES FROM NORTH
AMERICAN BIRDS *

H. J. VAN CLEAVE

INTRODUCTION

When Lühe created the genus *Arhythmorhynchus* (1911:47) he assigned to it but one species *A. frassoni* (Mol.). The following year in publishing the results obtained from a study of four immature specimens of *Echinorhynchus invaginabilis* von Linstow Lühe (1912:283) ascribed that species to the genus *Arhythmorhynchus* and in the same article accepted two American species, *Echinorhynchus uncinatus* Kaiser and *E. trichocephalus* R. Leuckart, as agreeing with his definition of the genus *Arhythmorhynchus*. Of these four species belonging to this genus but one is well known, namely, *A. frassoni* (Mol.). For the two American species not even the host is known, and while Kaiser (1893) has given minute details regarding the hooks of these two species, data concerning the embryos and many other points which are essential for a complete specific diagnosis are entirely wanting. Consequently it seems that concerning some of the points in the definition of the genus data are available for a single species only. It is not surprising that a generic diagnosis based upon the study of a very small number of species might later require emendation to permit including within the same genus species of obviously close relationship. Especially is this true in groups of parasites, such as the *Acanthocephala*, in which the organization of the body has been reduced to its simplest terms through perfect adaptation to the parasitic existence; for this same reduction eliminates large groups of organs and structures which in nonparasitic forms afford additional characteristics of diagnostic value.

Recently the writer (Van Cleave, 1913) found it advisable to emend the definition of the genus *Neoechinorhynchus* to permit including within it five species which were unknown to the founder of the genus. Similarly now after a study of new materials including two new species closely related to *Arhythmorhynchus frassoni* (Mol.) and *A. invaginabilis* (von Linst.) the writer has found it imperative to modify Lühe's original description of the genus *Arhythmorhynchus* (Lühe, 1911:47) to prevent exclusion from this genus of forms which under a natural

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system of classification could not be granted independent generic rank. The materials upon which the present study has been made were collected by Mr. Albert Hassall and deposited in the Collections of the U. S. Bureau of Animal Industry. Both species are represented in the collection by numerous fully mature individuals so that a complete study of the specific characteristics has been possible in both species. These new forms were found to deviate from Lühe's description of the genus *Arhythmorhynchus* in the following particulars: (1) the shape of the body; (2) the location of the testes with reference to the two regions of the body proper described by Lühe; (3) the shape of the membranes surrounding the hard-shelled embryos in the body cavity of the female. In the estimation of the writer these are placed in the order of their relative significance, the least significant first.

As Lühe has pointed out, the anterior region of the body in members of the genus *Arhythmorhynchus*, which in some species is an inflated oval region standing out in contrast to the smaller cylindrical posterior region (Figs. 1 and 4) contains relatively large numbers of subcuticular nuclei while the posterior region is devoid of subcuticular nuclei. Simple body shape has been so long recognized as a variable quantity by those working with *Acanthocephala* that little emphasis may justly be given it alone. However, when body shape has as an accompanying feature distinctive structural characteristics emphasis may be placed upon the structure as of diagnostic value though broad range of variation may occur in the gross outer form in which the structure finds expression. Therefore, in defining the genus *Arhythmorhynchus*, emphasis should be placed upon the difference in structure between anterior and posterior regions of the body rather than upon the difference in shape of these two regions, for the structure is constant in all species which have been examined though the body form is widely variable. For the males of this genus Lühe has specified that the testes occur in the anterior swollen region of the body (Fig. 1). Suspended as they are in the genital ligament running backward through the body cavity from the base of the proboscis sheath and with no intimate relationship to the body wall little of generic value may be placed upon the exact location of these organs in the body cavity. In one species at least (Fig. 4) the testes do not lie in the swollen region of the body as indicated in Lühe's diagnosis of the genus, but are located distinctly posterior to that region. The third point of difference, the shape of the embryonic membranes, presents the most radical point of divergence in the species under consideration from the original description of the genus. Lühe throughout his classification of the *Acanthocephala* has emphasized the importance of shape of the embryos and structure of their coverings as of marked diagnostic value. For *Arhythmorhynchus* he has specified in his characterization of that genus the presence of

three fully concentric membranes surrounding the embryo within the body cavity of mature females. His observations upon the embryos of *A. frassoni*, the only species of the genus for which sexually mature individuals were at that time known, corroborated the earlier record of de Marval (1904, Fig. 55) for the embryos of the same species. However in *A. brevis* and *A. pumilirostris* the writer has found two species which, though agreeing with Lühe's definition of the genus in all other essential characteristics, present a marked contrast in the structure of the embryos. In each of these species numerous fully mature females have been examined with the unvarying result of disclosing hard-shelled embryos in which the middle membrane has an outpocketing at each pole (Figs. 10 and 12).

In view of the foregoing details, wherein the two newly described species fail to agree with the original definition of the genus, two possibilities present themselves: either (1) a new genus should be established for these two species; or (2) the definition of the genus *Arhythmorhynchus* should be modified so as to include these forms. To the writer it seems unwise to create a new genus for forms which differ from an existing genus by but a single point of essential distinction: namely the shape of the membranes surrounding the embryos. Especially does this seem uncalled for in the case under consideration in which up to the present time, embryos were known for but a single species. Therefore it appears expedient to recast the definition of the genus *Arhythmorhynchus*.

REVISED DIAGNOSIS OF THE GENUS ARHYTHMORHYNCHUS

Acanthocephala with a spindle-shaped proboscis upon which the hooks are arranged not in radial but in bilateral symmetry since those on the dorsal and ventral surfaces of the same individual differ, though in varying degrees in different species. Anterior region of body sharply differentiated from posterior region in structure of body wall, especially in the presence of nuclei in the subcuticula of anterior region only. Portion of the anterior region of body proper spined. Spines entirely wanting on neck and on posterior region of body proper. Proboscis sheath a double-walled muscular sac inserted at the base of proboscis. Central nervous system near center of proboscis sheath. Cement glands very long, slender. Embryos in body cavity of female elongated oval with three membranes, all concentric or the middle one with an outpocketing at each pole. Sexually mature in the intestine of birds.

ARHYTHMORHYNCHUS BREVIS NOV. SPEC.

Body in both sexes with distinct oval enlargement comprising about anterior half. Posterior end distinctly smaller, elongated, cylindrical. Females 6 to 12 mm. long; maximum thickness 3 mm.; diameter of

posterior region about 1 mm. Males, 5 to 6 mm. long; maximum thickness, 1 to 1.5 mm.; diameter of posterior region, 0.5 to 0.75 mm. Neck naked, retractable, tapering toward proboscis, not sharply set off from body, 0.35 to 0.55 mm. long. Body for short distance just back of neck irregularly set with small number of spines 0.012 mm. long. Proboscis elongated with conspicuous expansion near center, 0.665 mm. long, 0.230 mm. in diameter at base, 0.190 mm. at tip, 0.340 mm. at center. Proboscis armed with eighteen longitudinal rows of hooks, usually fifteen in a row. Basal hooks nearly straight, slender, 0.047 mm. long. Heaviest hooks near middle of proboscis 0.041 to 0.047 mm. long, on ventral surface slightly larger than on dorsal. Hooks at tip slender, recurved, 0.047 mm. long. Cement glands long, narrow. Testes oval, slightly overlapping one another, in swollen part of body. Embryos 0.076 to 0.100 mm. by 0.024 to 0.030 mm. Middle of three shells of embryos heavy, with a rounded swelling at each pole. Host *Botaurus lentiginosus* (Montag.), intestine. Type locality Baltimore, Md., U. S. A.; Cotypes in collection Bureau of Animal Industry, Washington, D. C., Catalog No. 6302; and in the Helminthological Collection of the Department of Zoology, University of Illinois, Urbana, Catalog No. 16, 165.

The structure of the body wall in the genus *Arhythmorhynchus* presents numerous anomalies when compared with conditions found in other genera of *Acanthocephala*. The writer has made a study of some of these points, especially in the species *A. brevis*, the results of which follow. Lühe (1911: 47) has called attention to the peculiar distribution of the subcuticular nuclei in this genus and incidentally in a vague manner has referred to other differences between the anterior and posterior regions of the body. Figure 11 shows the shape, structure, and location of the subcuticular nuclei in a longitudinal section through the anterior region of a specimen of *A. brevis*. The entire subcuticula is a peculiar structure, presenting an appearance unparalleled in any other genus of *Acanthocephala*. In the anterior region of the body there may be easily recognized beneath the cuticula (*c*) a region in which small fibrillae run both longitudinally and radially (*sc1*). An intermediate more heavily granular zone (*sc2*) separates this region from the region of radial fibers (*sc3*) in which the subcuticular nuclei (*sn*) are contained. This last region, which Kaiser (1913, Plate 1, Fig. 1) in *Gigantorhynchus hirudinaceus* called the hypoderm, is bounded on its inner surface by a layer of circular muscular threads (*cmt*).

The longitudinal muscular layer in the anterior part of the body shows some most striking deviations from conditions usually found in the body musculature of *Acanthocephala*. The presence of large nuclei (*mn*) in, and of numerous finger-like fiber-bundles (*mf*) imbedded in an undifferentiated cytoplasmic envelop (*uc*) suggest a resemblance to

the nematode musculature. But this can be scarcely more than a suggestion since the orientation of the fibers is the opposite of that characteristic of the nematodes. Figure 11, a longitudinal section of *A. brevis*, shows these fiber-bundles in a position comparable to the view obtained in a cross section of a nematode. Though this agreement in fundamental structure of the muscle cells may indicate a relationship between the Acanthocephala and the Nematoda, yet the confusion in the arrangement of the fibers prevents ascribing to the argument any great phylogenetic importance.

Lühe in his characterization of the genus *Arhythmorhynchus* commented upon the slight development of the lacunar system of the subcuticula. In Figure 7, the writer has shown a portion of a tangential section through the subcuticula of *A. brevis*. A longitudinal canal (*lc*) is shown in its characteristic relationship with a circular canal (*cc*). In this species, at least, the canal system is well developed, though the extent and complexity of the subcuticular layer tend to make it inconspicuous.

In the posterior region of the body the body-wall presents its broadest departure in *A. brevis* from the conditions usually found in other genera. Here, as has been stated before, there are no subcuticular nuclei. The regions of the subcuticula (Fig. 8) agree in arrangement and general structure with those previously described for the same layer in the anterior part of the body. However, between the double row of circular muscle threads (*cmt*) and the body cavity is interposed a series of structures which are evidently modified continuations of the muscular system described for the anterior region of the body. In a longitudinal section, or in an optical section of a well prepared whole mount, this modified part has the appearance of a series of triangular elevations (*tr*) with the base of each triangle directed toward the layer of circular muscle threads. From the apex of each of these triangles is given off a fine membrane (*m*) which runs inward toward the longitudinal muscle sheath. Each of the triangular elevations is pierced by a canal (*ca*) about 0.025 mm. in diameter. These triangular ridges occupy only about one fourth the region between the circular muscular threads and the muscle sheath lining the body cavity. Most of the intervening space is open cavity intercepted at irregular intervals by very thin membranes (*ms*) of another series which do not take their origin or have their insertion in the triangular ridges. The open spaces between the membranes are in communication with the central body cavity as is especially shown by the presence within the chambers of large numbers of eggs and embryos (*e*) in various stages of formation.

Some of the muscles within the body cavity show a peculiar striation. Figure 6 represents a single fiber of one of the retractor muscles

greatly magnified. Regions of dark striations (*st*) alternate with bands of nonstriated structure, while the nucleus (*n*) is in a mass of undifferentiated cytoplasm at one side of the fiber.

ARHYTHMORHYNCHUS PUMILIROSTRIS NOV. SPEC.

Body of males and immature females with slight enlargement comprising about anterior fifth. Gravid females with posterior region of body enlarged, cylindrical, with irregularly distributed swellings. Females up to 30 mm. long. Maximum diameter fully gravid female, slightly posterior to middle of body, 1.5 mm.; diameter anterior region 0.9 mm. Neck naked, retractile, tapering toward proboscis; in size not sharply set off from body. Body for short distance behind neck set with small spines, 0.012 to 0.020 mm. long. Proboscis elongated, with conspicuous swelling near center; length 0.450 mm.; maximum breadth 0.180 mm.; breadth at tip 0.095 mm., at base 0.114 mm. Proboscis armed with sixteen longitudinal rows of hooks with fourteen or fifteen hooks in a row. Basal hooks nearly straight, thorn like, usually 0.035 mm. long. Heaviest hooks on ventral surface near middle of proboscis 0.030 mm. long. Hooks at tip slender, recurved, 0.030 to 0.035 mm. long. Cement glands in male extremely attenuated. Testes contiguous in region behind anterior swelling of body. Embryos 0.065 to 0.089 mm. long; 0.018 mm. wide; with three membranes, the middle one with an outpocketing at each pole.

Host *Botaurus lentiginosus* (Montag.), intestine. Type locality Washington, D. C. Cotypes in collection of Bureau of Animal Industry, Washington, D. C., Catalog No. 2076; and in the Helminthological Collection of the Department of Zoology, University of Illinois, Catalog No. 16, 166.

In its microscopic anatomy this species closely resembles that given for the preceding species. Figure 13, an optical section of *A. pumilirostris*, indicates the general distribution of the two types of subcuticular structure discussed under the morphology of *A. brevis*, while Figure 12 shows a single hard shelled embryo.

INTERRELATIONSHIPS OF THE SPECIES

Upon the basis of the characteristics of the proboscis hooks alone there is an indication of a natural division of this genus into two subgroups which make comparisons between species fairly certain even though the essential diagnostic facts for some species are not all known. One group consists of those species whose members possess a few extremely large hooks at the middle of the ventral surface of the proboscis; *A. frassoni* and *A. trichocephalus* fall within this group. In the second group the midventral hooks are but slightly larger than the

midlateral and middorsal hooks; to this belong *A. invaginabilis*, *A. brevis*, *A. uncinatus*, and *A. pumilirostris*. *A. brevis* and *A. pumilirostris* may be separated from *A. invaginabilis* upon the basis of the number of longitudinal rows of hooks upon the proboscis. For the last named species Lühe (1912:287) found twenty-two to twenty-four longitudinal rows of hooks. Eighteen are found in *A. brevis* and sixteen in *A. pumilirostris*. The separation of *A. uncinatus* is most sharply shown in a comparison of the size of the hooks. Kaiser (1893:15) found hooks upon the proboscis of *A. uncinatus* ranging from 0.056 to 0.120 mm. long while in *A. brevis* the writer has found the range in size of hooks to be from 0.030 to 0.047 mm., and in *A. pumilirostris* the longest hooks are 0.035 mm. long. *A. brevis* and *A. pumilirostris* are most readily separable one from the other by the fact that the former has the larger proboscis with eighteen longitudinal rows of hooks, while the latter has but sixteen longitudinal rows of hooks upon a much smaller proboscis.

At the end of his work on the Acanthocephala of the fresh waters of Germany, Lühe (1911:53) has considered a number of species which were insufficiently known to permit of classification in his system with certainty. Among these is a species *E. striatus* Gze. for which he has mentioned an apparent relationship with the genus *Corynosoma* through the shape of the embryos. Since this is the sole point where the present writer found the two species *A. brevis* and *A. pumilirostris* to differ from Lühe's description of the genus *Arhythmorhynchus* and since the figures and description of *E. striatus* agree also with that genus the writer can see no objection to including the species *striatus* within the genus *Arhythmorhynchus* as emended in the present paper.

KEY TO THE SPECIES OF ARHYTHMORHYNCHUS REPORTED FROM NORTH AMERICA

- 1 (2) Hooks on mid-ventral surface of proboscis conspicuously larger than any others.....*A. trichocephalus* (R. Leuckart)
- 2 (1) Hooks on ventral surface of proboscis not conspicuously larger than on other surfaces.....3
- 3 (4) Longest hooks more than 0.100 mm....*A. uncinatus* (Kaiser)
- 4 (3) Longest hooks not more than 0.050 mm.....5
- 5 (6) Proboscis with sixteen longitudinal rows of hooks; embryos 0.065 to 0.089 mm. long and 0.018 mm. wide.....
.....*A. pumilirostris* Van Cleave
- 6 (5) Proboscis with eighteen longitudinal rows of hooks, embryos 0.076 to 0.100 mm. long, and 0.024 to 0.030 mm. wide.....
.....*A. brevis* Van Cleave

SUMMARY

Two new species of Acanthocephala from the intestine of *Botarurus lentigenosus* show close relationship to *Arhythmorhynchus frassoni*. They fail to agree with Lühe's definition of the genus *Arhythmorhynchus* in: (1) shape of the body; (2) location of the testes; (3) shape of the membranes surrounding the hard-shelled embryos. The original characterization of the genus is emended to include these forms which possess every other essential characteristic of the genus.

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EXPLANATION OF PLATES

All figures drawn from permanent, stained, balsam mounts with the aid of a camera lucida.

PLATE 1

- Figs. 1 to 3.—*Arhythmorhynchus brevis* nov. spec.
- Fig. 1.—Immature male, entire.
- Fig. 2.—Profile, dorsal surface, proboscis of mature male.
- Fig. 3.—Profile, ventral surface, same proboscis as in Figure 2.
- Figs. 4 and 5.—*Arhythmorhynchus pumilirostris* nov. spec.
- Fig. 4.—Male, entire.
- Fig. 5.—Profile, anterior end of body of same individual as shown in Figure 4.
4. Proboscis hooks same magnification as Figures 2 and 3 of *A. brevis*.
- Figs. 6 and 7.—*A. brevis*.
- Fig. 6.—Muscle fiber from one of the retractor muscles.
- Fig. 7.—Portion of tangential section through cuticula and subcuticula showing relations of longitudinal (*lc*) and circular (*cc*) canals.

PLATE 2

- Figs. 8 to 11.—*A. brevis*.
- Fig. 8.—Portion of body wall in posterior region. Sagittal section. For details see text.
- Fig. 9.—Spines from anterior part of body wall.
- Fig. 10.—Embryos from gravid female.
- Fig. 11.—Portion of body in anterior region. Sagittal section. For details see text.
- Figs. 12 to 14.—*A. pumilirostris*.
- Fig. 12.—Embryos from gravid female.
- Fig. 13.—Anterior end of body, optical section, showing relative differentiation and distribution of subcuticula.
- Fig. 14.—Spines from anterior part of body.

PLATE 1

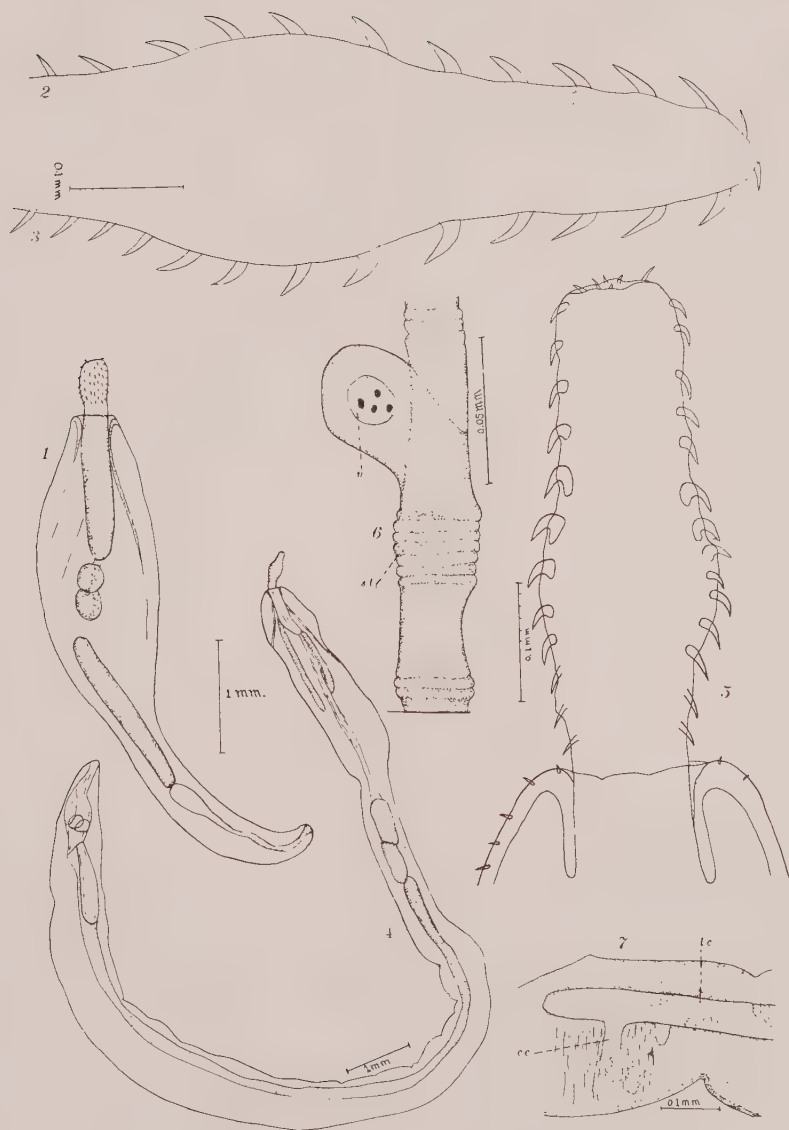
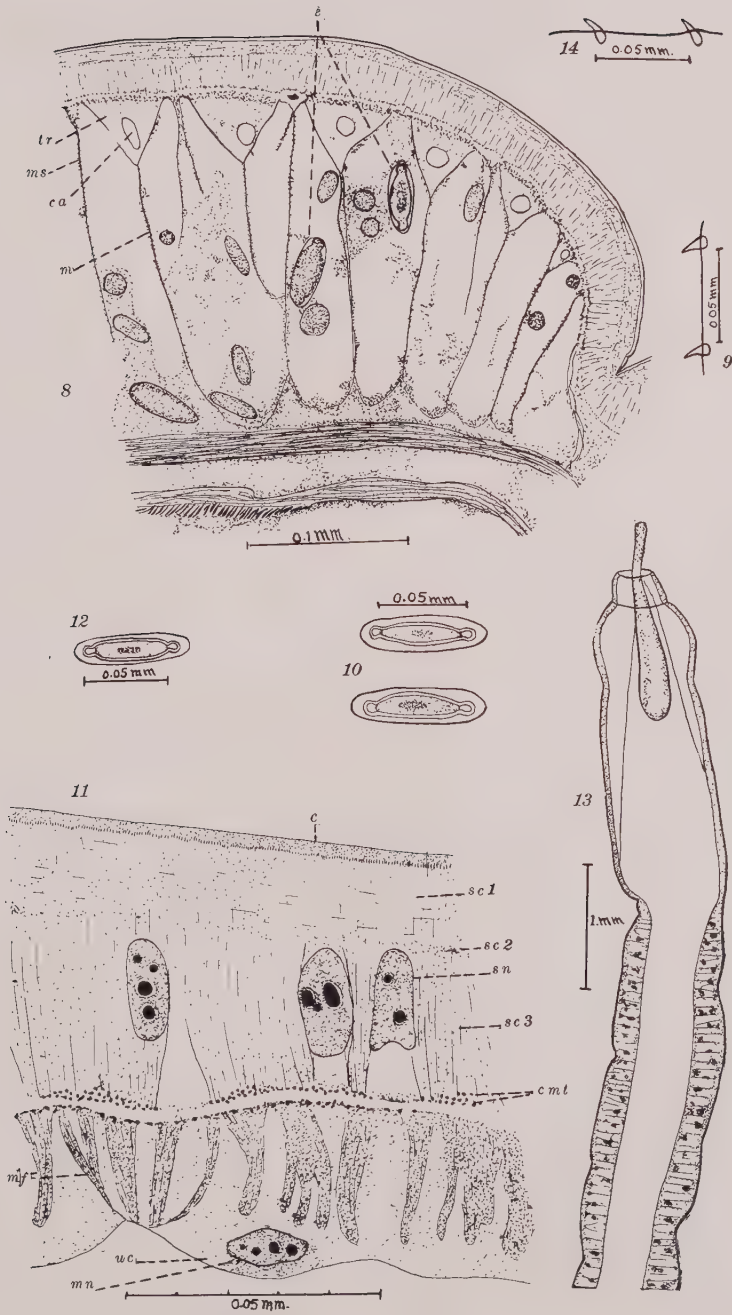


PLATE 2



SOME NOTES ON THE ENCYSTED LARVA OF THE LUNG DISTOME

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In a former article (1916) I reported on (1) the discovery of the intermediate hosts (crabs) of the lung distome in Japan; (2) species of the intermediate hosts in various districts of our country; (3) the frequency of occurrence of the encysted larvae (cysts) in various crabs; (4) morphology of the encysted larva; (5) the animals, experimentally fed with the cysts, etc. The report to be given in the following pages is a part of the results obtained by subsequent study on the cysts of the lung distome in crabs, especially *Eriocheir japonicus* (de Haan).

DISTRIBUTION AND MIGRATION OF CYSTS IN THE BODY OF AN INTERMEDIATE HOST

The encysted larvae are found in various parts of *E. japonicus*, namely, muscles, hypodermis, gills, liver and other organs; of these, muscles and gills are most abundantly infected. The absolute number of cysts is greater in the muscles than in the gills, but the relative number is inverse, because the volume of the muscles is much larger than that of the gills. The cysts in the gills are found only along a limited portion of blood vessels running longitudinally on the median line of their upper surfaces. In the muscles the cysts are found most frequently and most abundantly in the base of each appendage. Numerous cysts are often found in the muscles near the basipodite of each appendage, even in the cases in which a few or none of cysts are found in other parts of the musculature.

From the abundance of the cysts in gills and near their attachment, the basipodite of each leg, and from the system of blood circulation in the crab, I am inclined to believe that the encysted larvae have a tendency to migrate toward the gills from all parts of body by means of the blood circulation. It was experimentally proved that the cyst has the ability to migrate through the various tissues of the crab, although the rate of migration is very slow. On the other hand, the circulatory system of the crab is open, as the distal ends of the arteries open into the tissues of the body and thus all tissues are bathed in the blood. The venous system begins not with capillaries, as in a closed system, but with lacunae, lying irregularly among the tissues. The lacunar spaces in the tissues communicate with one another at first, and gradu-

ally form a canal system after union of several lacunae from different parts; ultimately these grow into the venous vessels which run toward the gills to purify the blood. The blood current among the tissues and in the vessels of the venous system surely facilitates the migration of the cysts toward the gills. If this supposition is right, it explains clearly why the cysts are found abundantly in the small blood vessels in the gills and in the muscle near the base of each appendage.

Thus the venous vessel is the most convenient course by which the cysts migrate toward the gills. For what purpose do the cysts migrate to the gills? Is there any necessity for the cysts to migrate to the gills? It is most favorable, I believe, for the cysts to migrate to the gills in order to facilitate further development of the encysted larvae by getting into the final host. On the whole, there are two ways by which the cysts may be taken up by the final hosts—human beings or other animals as dog, cat, etc.—namely: (1) their consumption as a food in an uncooked crab; (2) being taken with food and drink infected with cysts liberated into water from the intermediate host. In the second method of infection it is necessary for the cysts to escape into the water from the infected crab. The gills are the most convenient point at which the cysts can escape easily into the water, because the organ is always being laved by water and the blood vessel containing the cysts is separated from the outside water only by the very thin membranous wall. Thus it is reasonable to think that the cysts in various parts of the intermediate host migrate through the tissues carried by the blood current in the venous vessels toward the gills from which they may be discharged into the water.

It is questionable in my mind whether the cysts in a crab (*E. japonicus*) escape into the water naturally and actively to secure an opportunity of being taken up by the final host. In Corea, R. Moriyasu, E. Arima, and M. Tanaka proved experimentally the natural and active escape of cysts in the case of *E. japonicus*. In Formosa, K. Nakagawa obtained the same results as Moriyasu in the case of *P. obtusipes* (Stimpson). In Japan proper, R. Ando also proved experimentally that the result is quite the same in the case of *P. dehaanii* (White). All these writers made their experiments by approximately similar methods, namely, putting ten to thirty specimens of a crab which seemed to be infected with the cysts into cylindrical glass vessels with a little water. Renewing the water once or twice a day, they searched for cysts. In these examinations they all found the cysts more or less numerous, and hence concluded that the cysts escaped naturally and actively from the body of crab. In the case of *P. dehaanii* and *P. obtusipes*, it is possible that the cysts in the crab may escape into the water naturally and actively, because in these intermediate hosts the cysts are often found

attached to the outer surface of gills, as I reported in the former paper (1916).

I have also made some experiments to prove the natural and active discharge of cysts from the crab. There were two sets of experiments: 1. I prepared a glass aquarium 75 cm. long, 27 cm. wide and 29 cm. deep, provided with three small exits on the bottom, the upper side being open and covered by metal gauze when necessary. Twenty crabs or more of moderate size were put into the aquarium, and water was permitted to flow in by a pipe and out through three exits which were closed by two or three sheets of gauze in order to prevent the escape of the cysts. I examined the sediment on the bottom occasionally for cysts and have often found them among materials there. 2. I put one or two specimens of crab into a cylindrical glass vessel 18 cm. in diameter and 15 cm. deep, pouring in water to a depth of 3 cm. or more. I prepared five such vessels, and renewed the water once or twice a day. This set of experiments was continued three months, having been started October 4 last year. In this long-continued experiment, only one cyst came under my observation. In these experiments I used the crabs *E. japonicus* (de Haan) from Tomioka, *Tokushima Prefecture*, which were abundantly and frequently infected with the cysts of the lung distome.

In the first set of experiments I frequently found numerous cysts among other sediment. I have occasionally found dead crabs in the aquarium and pieces of legs and other parts of the body were always present in the material on the bottom of the vessel. It is reasonable to think that the cysts in the crab are easily discharged from the body when the crab is dead or any part of body is accidentally injured. Hence from observation of the above facts I believe that these free cysts in the aquarium were unnaturally and passively discharged from the body by occasion of death or some injury.

When the crabs used in the second set of experiments were dead the substitute crabs were usually transported from the aquarium of the first set. It is even possible that the one cyst which I found in the second was not naturally and actively discharged from body of crab itself, but was carried attached to some part of the body from the aquarium in which I had proved the presence of cysts as stated above. The thickly haired forceps of the crab may be a good carrier of cysts, adhering to it even in case the crab had been carefully washed to remove attached particles.

In considering the facts observed in the above two sets of experiments one may say that if the cysts in the first aquarium had been naturally and actively discharged from the crabs I should have found more numerous cysts in the vessels of the second series than were found actually. But in reality, there was only one cyst in the vessels

of the first set during a long time. Thus I conclude from my own experiments that cysts in the intermediate host (*E. japonicus*) are not naturally and actively discharged from the body, but are often expelled unnaturally and passively by death of the crabs or some injury. In nature there are many occasions favorable for cysts escaping from crabs unnaturally and passively, namely, death of the crabs, frequent injuries by the fierce quarrels of the warlike crabs, breaking legs in slight disturbances, and accidental injuries in the period of moulting, etc.



Japanese River Crabs which serve as intermediate hosts for *Paragonimus westermanii*. A. *Sesarma dehaani* M. Edwards. B. *Potamon dehaanii* (White). C. *Potamon obtusipes* (Stimpson). D. *Eriocheir japonicus* (de Haan). Photographs by Mr. Koyama.

LONGEVITY OF CYST IN WATER

For studying the transfer of this cyst to a final host, it is most important to know how many days the cyst can be kept alive naturally in water. I have made the following experiments to determine this matter: To keep the cysts in water in a state as similar to natural conditions as possible, I prepared a small glass aquarium of 30 cm. long, 20 cm. wide and 17 cm. deep with the bottom provided with one small exit. Water was constantly pouring into it by the inflow pipe and flowing out through the exit on the bottom, so the water in the aquarium was always moving and being renewed as in a running stream. For convenience in examining perfectly changes in the cysts and counting accurately the number of cysts dead or alive, I used as a case for holding them a glass tube opening at both ends covered by one or two

sheets of gauze and filter paper to prevent the cysts escaping from the tube but to permit the water to flow in and out though not freely.

(A) I put forty-two cysts from the gills of *E. japonicus* in a tube whose ends were closed by gauze. The tube was placed in the aquarium October 30 and taken out for examination November 12, having been in water thirteen days.

(B) Twenty-five cysts from the gills of the same species of crab were put in a tube, one end of which was closed by layers of gauze and two layers of filter paper and the other end by two layers of gauze and one layer of filter paper. The tube was kept in the aquarium from November 12 to 27, an interval of fifteen days.

(C) Twenty-five cysts from the gills and muscles of the same species of crab were put in a tube whose ends were closed by two layers of gauze and two layers of filter paper. The tube was left in the aquarium from November 12 to December 10, or twenty-eight days.

(D) November 15 I removed the cysts with surrounding tissues of the host from the gills and muscles of a specimen of *E. japonicus* that had died November 12. Twenty of these cysts were put in a tube whose ends were closed as in Case C. The tube was immersed in the aquarium during twenty-five days from November 15 to December 10.

The results of these experiments are listed as follows:

Case	Total Number	Living One	Dead One	Cyst Only	Percentage	Days
A	26	10 (in cyst) 4 (outside)	4 (in cyst) 1 (outside)	4	53.8	13
B	25	4 (in cyst) 1 (outside)	5 (in cyst) 1 (outside)	14	20.0	15
C	25	(All were dead and decomposed)			28
D	20	2	2	14	10.0	25

In Case A twenty-six out of forty-two cysts were found in the tube and the remaining were lost. The loss may be perhaps due to having closed both ends of the tube with gauze only. To avoid this defect in Cases B, C and D, I had used both gauze and filter paper for closing the tube ends, the latter being placed inside of the former.

Cysts containing living larva were not all perfect, some of them being slightly broken and the others so widely broken that the larva was creeping out. I found there were living worms also in various stages. Some of them were actively moving with the light red pigment in the body as observed in fresh larvae, others moved slowly, and some others appeared dead, having no apparent motion. In the last group the light red pigment was greatly reduced or entirely absent. Various gradations of morphological change and putrefaction were observed in

dead worms. In almost all the cysts, whether the worm was alive or dead, swarmed an immense number of flagellata of various species.

From my experiments above it is evident that the encysted larva may be kept alive relatively long in water. If a larger tube be used instead of a small one as in my experiments and both ends of the tube be closed by other suitable materials which make the circulation of water in the tube as perfect as possible under the conditions that retain the cysts, putrefaction of the cysts and their surrounding host tissues would be delayed and consequently the cysts would remain alive for longer time. Therefore we may conclude that cysts in water remain alive at least for thirty days under natural conditions.

From my other experiments it is known that cysts in the crab may be kept alive for a week in the winter season, the gills and other inner parts of the crab being exposed to an air by taking off the carapace.

METHOD OF INFECTION

There are two ways in which the human host may be infected with encysted larvae from the crab: (1) by taking as food an uncooked crab infected with living cysts; (2) by taking with food and drink living cysts discharged from the crabs. Which of these two ways of infection is common may be quite different in various districts of the country, varying according to the species of intermediate host and to the custom of people in the district. One intermediate host, *E. japonicus*, is edible and used as food in all districts of Japan, but it is generally eaten cooked—boiled, roasted or fried—and is rarely used uncooked. Another crab, *P. dehaanii*, is also edible and eaten cooked or uncooked in general. In some districts it is customary to use it uncooked in certain season of year. People in these districts are easily and commonly infected by eating uncooked crabs and a large percentage of those people are found to be afflicted with lung distomiasis. *S. dehaani* is not taken as food and human infection will be brought about by the second method in the districts where *S. dehaani* happens to be the only intermediate host present.

For prophylaxis in the disease caused by the lung distome the following are necessary conditions: Not partaking of uncooked crabs and other foods washed in water in an infected district. Not drinking unboiled water in such district.

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CYLINDROTAENIA AMERICANA NOV. SPEC. FROM THE
CRICKET FROG *

MINNA E. JEWELL

In the fall of 1914, while looking for parasites, I found a cestode in the intestine of a cricket frog, *Acris gryllis*. Further collections were made and the repeated occurrence of the tapeworm showed that it was not merely incidental but a regular parasite in the host mentioned. This discovery was particularly interesting because of the rarity of cestodes, either species or individuals, in amphibians. So far as I have been able to ascertain, only five cestodes have yet been described from amphibians, and of these only two, *Taenia dispar* Goeze (1782), and *Taenia pulchella* Leidy (1851), are from Anura. No cestodes have ever been reported from a member of the genus *Acris*. For these reasons it was considered worth while to make a morphological and systematic study of this new form, the results of which are presented in the following paper.

I wish to express my thanks to Prof. Henry B. Ward for the use of his library and of materials from his private collections and for many helpful suggestions.

Aside from some fifty specimens I obtained from cricket frogs collected from a drainage ditch north of Urbana, Ill., specimens were also examined from *Rana pipiens* collected by W. W. Cort at Douglas Lake, Mich., and by R. G. Hall from Crystal Lake, Urbana; from *Rana virescens* collected by H. W. Duncanson near Peru, Neb., and from *Bufo lentiginosus*, locality unknown. Much of this material had been identified as "*Taenia dispar*" on the basis of its general form and of its host, but comparison of these specimens with specimens of *Taenia dispar* sent from Neuchâtel, Switzerland, by Dr. Otto Fuhrmann, showed conclusively that the American worms are a distinct species.

Taenia dispar was originally reported by Goeze from toads and frogs in Germany. He described it as being 6 inches long, cylindrical, of greatest diameter at the anterior end and diminishing gradually to a thread-like posterior end. The name "*dispar*" was suggested by this unusual shape. The color is white except at the posterior end, where it is brownish. Proglottids are distinct only near the posterior end in which region they are filled with numerous brown bodies. All of the proglottids are enclosed in a thin transparent membrane, which is

* Contributions from the Zoological Laboratory of the University of Illinois, under the direction of Henry B. Ward, No. 67.

clearly visible between the proglottids at the posterior end. Observations were made on living material placed in water and the great activity of the worm noted.

O. Schmidt (1855) studied some eighty or ninety specimens obtained from *Rana temporaria*. He pictures a worm in which the neck is pronounced, being about one half the diameter of the scolex and two fifths the diameter of the body where the testes are at their fullest development. Failing to find the female organs he apparently mistook the testes for ovaries, and while he gives us a description and figure of what is unmistakably an oval cirrus pouch, he fails to recognize it as such, but considers it a part of the female reproductive system. He describes in detail the development of the embryo and subsequent formation of capsules, each surrounding three embryos. Of these capsules he found nineteen to twenty-five in each proglottid, first arranged in the form of a circle, but later becoming scattered irregularly through the proglottid.

Fuhrmann (1895) summarizes the contributions of previous workers and adds a careful and detailed description of his own, a summary of which follows:

Taenia dispar is characterized by its cylindrical form and by the fact that its diameter is greatest at the anterior end and diminishes gradually toward the posterior end. The scolex is unarmed and is not separated from the body by a neck. The pores are lateral and the cirrus and vagina pass dorsal to the longitudinal excretory vessels and main nerve trunk (Textfig. A). The testes are dorsal, two in number, and measure 0.108 by 0.045 mm. The cirrus sac is a strongly muscular organ, having a length of 0.27 mm. and a diameter of 0.026 mm. It terminated in a retractor which extends to the muscle layer on the opposite side of the proglottid.

The female genital organs occupy the ventral part of the proglottid. The ovary is spherical, 0.081 mm. in diameter, surrounded by a delicate membrane and filled with forty to ninety cells 0.014 mm. in diameter. The vitelline gland is also spherical, but its cells are much smaller than those of the ovary. No shell gland was observed. The uterus first appears as a mass of dark cells between the ovary and testes. At its fullest development it is a large horseshoe-shaped organ, the dorsal part of which crowds the remnants of the testes against the dorsal muscles. The uterine wall soon degenerates and the eggs receive their second and then their third membranes from the parenchyma. The parenchyma now becomes concentrated about groups of three or sometimes four eggs, enclosing them in a parenchymatous capsule. These egg capsules, thirteen to thirty in number, become scattered irregularly through the proglottid.

It is noteworthy that there are marked discrepancies between the figures and descriptions of *Taenia dispar*, contributed by Goeze and Fuhrmann on the one hand, and O. Schmidt on the other. While the circular arrangement of the eggs described by Schmidt and the horseshoe-shaped arrangement described by Fuhrmann might readily be accounted for as differences in observation, there are more important differences which cannot be so readily explained. Whereas Goeze

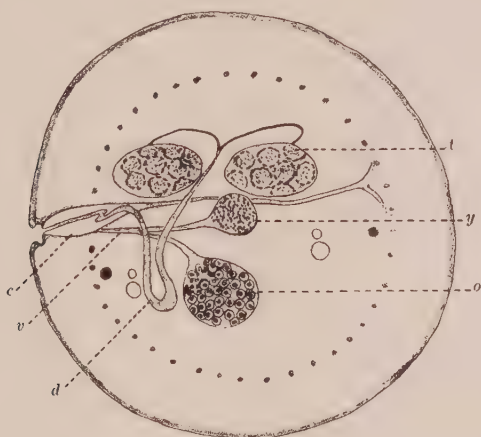


Figure A

Cross section of a mature proglottid of *Taenia dispar*. (After Fuhrmann, 1895); *t*, testes; *c*, cirrus pouch; *d*, vas deferens; *o*, ovary; *u*, uterus; *v*, vagina; *y*, vitellaria.

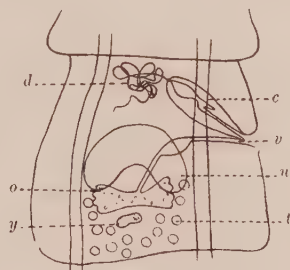


Figure B

Mature proglottid of *Paruterina angustata*, showing the arrangement of organs characteristic of the sub-family Paruterinae. (After Fuhrmann, 1906.)

and Fuhrmann both picture and describe *Taenia dispar* as neckless, having its greatest diameter at the anterior end and diminishing gradually toward the posterior end, Schmidt, as noted above, gives a picture of a worm with a pronounced neck and with its greatest diameter near the posterior end. Further, Fuhrmann describes the cirrus sac as being almost ten times as long as broad, while Schmidt pictures an oval

cirrus sac not more than twice as long as broad. These discrepancies would suggest the possibility that the form worked upon by Schmidt was not *Taenia dispar*, and that the number of taenian species found in amphibians is greater than has heretofore been supposed.

Weinland (1858) attempted to put this form in a new genus, *Proteocephalus*, a position which subsequent workers have shown to be untenable. Lühe (1899) proposed for *Taenia dispar* the generic name *Nematotaenia*, suggested by the cylindrical form and unsegmented appearance of the body. Ransom (1900) gives the following diagnosis for the genus *Nematotaenia*:

Paruterinae; scolex unarmed without rostellum. Segmentation of strobila distinct only at the posterior end. Strobila circular in cross section. Genital pores alternate; genital canals pass dorsal to the longitudinal excretory vessels and nerve. Uterus horseshoe shaped, disappears early. Eggs through the action of numerous parauterine organs become inclosed in egg capsules, three or four in each capsule. Adults in amphibia. Type species *Taenia dispar* Goeze 1782.

Stiles and Hassall (1912) record the following as hosts of *Taenia dispar*: *Bufo americanus*, *Menobanchus maculatus*, *Bufo vulgaris*, *Rana pipiens*, *Rana temporaria*, *Ascolobates mauritanicus*, *Bufo cinereus*, *Bufo fuscus*, *Bufo lentiginosus*, *Hyla arborea*, *Necturus maculatus*, *Pleobetes fuscus*, *Platydictylus guttatus*, *Rana halecina*, *Salamandra atra*, *Salamandra maculata*. It is likely that in some of the above cases, the worm found was not *Taenia dispar*, but the species under consideration in this paper or some form much like it.

Taenia pulchella is known only from the rather meager description given us by Leidy (1851), which runs as follows:

White, without admixture of any other color, variable, usually broadest anteriorly. Head quadrilateral, subclavate, obtusely rounded, broader than neck. Acetabula circular, cup shaped, lateral and opposite, sessile protractile. Neck very long, cylindroid. Articuli containing several colorless globules; anteriorly subglobular or transversely oval; posteriorly moniliform, longitudinally oval, or cylindroid and centrally incrassate. Entire length, 50.8 to 238.6 mm. Scolex, diameter, 0.34 mm. Acetabula, 0.127 to 0.153 mm. Anterior proglottids, length, 0.34 mm.; diameter 0.254 to 0.53 mm. Ripe proglottids, length, 0.53 to 0.57 mm.; diameter, 0.19 to 0.34 mm. Host, *Bufo americanus*.

Closely resembles *Taenia dispar* Goeze, found in *Bufo viridus*, etc., but it is relatively longer and narrower and is never colored.

Morphology of the New Species.—In making and tabulating measurements, the worms from *Acris gryllis* were found to fluctuate about a different mode from those from *Rana pipiens*, being usually smaller; however, since every gradation in size has been found and the larger worms from *Acris gryllis* are larger than the smaller ones from *Rana pipiens*, and since also it has been observed in *Acris gryllis* that in cases of heavy infection mature worms are much smaller than those found in lightly infected hosts, sometimes not more than one half the diameter, the author feels no hesitation in saying that only one species is concerned.

Adult worms bearing ripe proglottids, from *Acris gryllis*, vary in length from 25 to 40 mm. when in a state of moderate extension. Young worms 1.5 mm. in length were repeatedly found in the intestine. The worms from *Rana pipiens* were not observed alive, but from preserved materials their length may be estimated to have reached a maximum of 80 mm.

The most characteristic feature of the worm, noted upon a superficial examination, is its cylindrical form. The color is glistening white throughout the entire length. The scolex is spherical, 160 to 200 μ in diameter in the region of the suckers, which have a diameter of from two fifths to one half that of the scolex. Thus in one scolex having a diameter of 180, the suckers are 97 μ . The neck is long and has a diameter of 130 to 150 μ . In a typical specimen from *Acris gryllis* 37 to 40 mm. in length, the neck has a diameter of 134 μ . The first appearance of the reproductive system is as a dark streak down the center of the worm about 5 mm. behind the head. Here the diameter is still 134 μ .

Soon the line of undifferentiated cells becomes broken into triangles, having their bases directed laterad and their species alternating with each other in the median line. Six mm. behind the head the differentiation of the testes becomes apparent. In this region the proglottids have a length of 9 μ and a diameter of 162 μ . Eleven mm. behind the head the proglottids are mature and the first eggs are passing into the uterus. Here the proglottids measure 20 by 157 μ . The greatest diameter of the worm is found where the uterus has reached its fullest development and the para-uterine organ is forming, about 22 mm. behind the head. In this region the proglottids are 40 to 45 μ long and 180 to 200 μ in diameter. When the worm is contracted the diameter may be 350 μ .

Soon after, about 24 mm. from the head, the proglottids begin to elongate rapidly and indications of external segmentation appear. They now have a length of 54 and a diameter of 135 μ . From 27 to 36 mm. behind the head the segmentation is very distinct. The proglottids measure 82 by 108 μ and break off easily. The last few proglottids of a strobila and the detached proglottids frequently have a length much exceeding their diameter, 146 by 72 μ to 178 by 74 μ . In specimens from *Rana pipiens* the proglottids attain a maximum diameter of 270 μ and ripe proglottids a length of 340 μ and diameter of 250 μ . Detached ripe proglottids have been found singly and in groups of from two to five in the cloaca of the host.

In living material the parenchymatous para-uterine organs which contain the oncospheres appear as two transparent spherical bodies in the center of each proglottid.

The cuticula is from 3 to 4 μ thick, and composed of three layers, the central one of which is thinnest. Beneath the cuticula is the usual

basement membrane and parenchyma. The subcutaneous muscles are weakly developed, the longitudinal muscles are pronounced, dorso-ventral muscles appear to be entirely wanting.

The ventral excretory canals vary in diameter from 3.5 to 12μ , usually from 5 to 7μ in parts anterior to the appearance of external segmentation. The dorsal canals vary in diameter between 1 and 4.5μ . They are but little smaller than the ventral canals in the region of the scolex, but are insignificant throughout the remainder of their length. The usual median excretory bladder is clearly visible at the posterior end of young specimens.

All of the organs of the reproductive system, with the exception of parts of the cirrus and vagina, are confined to the medullary region of the proglottid. The genital pores are lateral and alternate somewhat irregularly, though with a marked tendency toward regularity. Thus in one instance twenty-four pores alternate regularly, then two are on the right margin and the next two on the left; then four alternate regularly, two are at the right, five alternate regularly and two more are at the right, twelve alternate regularly and two are at the left, etc. More than two pores have never been observed to occur successively on the same side.

The cirrus and vagina pass dorsal to the main excretory canals and nerve trunk. The male organs occupy the dorsal part and the female organs the ventral part of the proglottid (Fig. 7). The single testis is situated dorsally on the aporal side of the proglottid. It varies from 26 to 34μ in diameter, being usually about 29μ at its greatest development, and is spherical except when anteroposteriorly compressed by the contraction of the worm. From it the vas deferens leads with but few undulations directly to the cirrus. This latter organ is surrounded by a thick club-shaped cirrus pouch 36 to 44μ long and 13 to 17μ in diameter. The cirrus pouch, vas deferens, and female organs are enclosed in a delicate sheath.

The vagina opens from the genital cloaca posterior to the male orifice and follows the cirrus inward. Near the end of the cirrus sac the vagina begins to curve ventrad. It meets the duct from the vitelline gland and the very short oviduct about the level of the principal nerve trunks. The single spherical ovary lies in the ventral half of the medullary region. It has a diameter of from 24 to 34μ , and contains from eight to sixteen large, spherical, loosely arranged cells 9μ in diameter, surrounded by a membranous capsule. The vitelline gland lies dorsolateral to the ovary and in the median line. It is spherical, 18μ in diameter, and composed of large deeply staining cells. The vitelline duct passes laterad, meeting the oviduct in an enlargement at the point of formation of the uterine duct. No special muscular oötype has been observed. A mass of deeply staining cells dorsal to

the vitelline duct is the anlage of the uterus. After fertilization the distal end of the oviduct becomes dilated and filled with sperm and yolk cells through which the egg must pass before entering the uterus.

The ova, when mature, pass in rapid succession through the oötype and into the uterus so that the ovary and vitelline glands soon disappear entirely. The uterus, an oval sac, lies on the pore side of the proglottid with its long axis directed dorsiventrally. At its fullest development it attains a size of 40 by 24 μ . The eggs at the time they enter the uterus may be surrounded by a transparent membrane, though groups of ova and yolk cells around which no membrane has yet formed are frequently found in the uterus. The complete eggs have a mean diameter of 12 to 14 μ .

The parenchyma on the aporal side of the uterus now becomes arranged as a meshwork of heavy deeply staining strands running parallel to the long axis of the uterus. This is the beginning of the parenchymous structure which, following Fuhrmann, I shall term the *para-uterine organ* (Fig. 2).

The growth of the para-uterine organ is rapid, and it soon appears as two truncated cones, one dorsal and one ventral, their bases lying against the uterus, which has become much flattened, and their apices extending almost to the circular muscles on the opposite side (Fig. 3). The basal portion of the cones is composed of a meshwork of fine dorsiventrally directed fibers. The apical parts are surrounded by heavy deeply staining fibers, among which lie numerous dark nuclei.

Meanwhile the eggs have initiated cleavage and have developed their second membrane, a thick deeply staining capsule, while the uterus, which was pushed close against the eggs by the growth of the para-uterine organ, has broken down into a number of tertiary capsules surrounding the individual embryos.

With the rapid elongation of the proglottid (Figs. 4 and 5) the position of the cones is shifted so that their longitudinal axes correspond very nearly to the longitudinal axis of the worm. Their apices lie in the anterior end of the proglottid and their basal portions, in which are the embryos enclosed in their uterine capsules, occupy the posterior part of the proglottid. At the same time the apical portions of the cones acquire well-defined walls and become somewhat constricted from the basal portions, while the spongy fibers which have filled them disappear leaving them hollow. By the time the proglottids have become distinctly set off, the apical portions of the cones appear as two thick-walled hollow spheres 20 μ in diameter, lying one dorsal, the other ventral, in the anterior end of the proglottid, while the meshwork of lamellated fibers has largely disappeared from the interior of the basal portions of the cones. At this time the embryos have a diameter of 20 μ and have developed the six hooks characteristic of the tape-worm oncosphere.

The oncospheres now begin to migrate forward into the spherical capsules of the para-uterine organ, which grow rapidly to a diameter of 124 to 130 μ (Fig. 6). At the time of the separation of the proglottids those embryos which have not yet migrated into the para-uterine capsule are usually set free by the tearing open of the end of the proglottid, so that a detached proglottid, when found in the cloaca of the host, frequently contains not more than five to seven oncospheres (Fig. 9).

The development of the para-uterine organ just described bears many resemblances to that described for *Metroliasthes lucida* by Ransom (1900). The chief differences are in the relative size and duration of the uterus and the number of para-uterine organs formed. In the form under discussion, as noted above, the uterus is relatively small and breaks down into membranes surrounding the embryos long before the development of the oncospheres is complete or the para-uterine capsule is ready to receive them. In *Metroliasthes lucida*, quoting Ransom, "at the height of its development the uterus occupies almost the whole of the inner parenchyma back to the genital pore and bulges out the proglottid wall dorsally and ventrally," and the uterus does not degenerate until the six-hooked embryos have taken up their final position in the para-uterine capsule. As to the number of para-uterine capsules formed, while in the form under discussion there are two, *Metroliasthes lucida*, although possessing a two-lobed ovary, has but one.

Fuhrmann (1906) has given in less detail the development of the para-uterine organ in *Paruterina angustata* and *Culcitella rapaciola*, (1908a) of *Anonchotaenia globata* and (1909) of *Biuterina clavulus*. Cholodkovsky (1906) has given a brief account of the formation of the para-uterine organ in *Rhabdometra tomica*. All of these forms resemble *Metroliasthes lucida* in that the uterus persists until the oncospheres have passed into the single para-uterine organ. *Taenia dispar*, on the other hand, resembles this form in that the uterus breaks down early, but far exceeds it in the number of para-uterine organs, of which there are from thirteen to thirty.

While the form under discussion bears some likeness to *Taenia pulchella* Leidy 1851, such as its occurrence in an anuran, its long neck, white color and cylindrical form, this similarity is far too generalized to establish identity. Since I have been unable to secure for comparison any of Leidy's material, which is reported to be no longer in existence, I must leave open the question of the possible identity of the two forms and treat this as a new species.

Fuhrmann (1908b) has revised the classification of the Cyclophylloids. Of his seven families it is the *Dilepinidae* with whose characters this worm agrees. The family is defined as follows: "Rostellum

usually armed, suckers unarmed, genital pores marginal, genital organs single or double in each proglottid." This family contains twenty-eight genera, which Fuhrmann has separated into three subfamilies on the basis of the character of the uterus.

The subfamily *Dilepinae* contains the genera in which the uterus is sac-shaped or has simple lobes. In most the uterus persists. The subfamily *Dipylidiinae* includes the genera in which the uterus breaks up into parenchymatous capsules which contain one or more oncospheres. The subfamily *Paruterinae* includes those genera in which a parenchymatous para-uterine organ is formed into which the embryos later penetrate. The enclosure of the embryos in the para-uterine capsule places the worm under consideration in this paper in the subfamily *Paruterinae*.

A comparison of the description of this form, given above, with the description of *Taenia dispar* given by Fuhrmann, reveals striking resemblances between the two (Fig. 7 and Textfig. A). Alike they are characterized by their cylindrical form and late differentiation of proglottids. The ovary and vitellaria are spherical and ventral, the vitellaria, however, being dorsal to the ovary. The testes are large, dorsal and of a definite and limited number, one in this form, two in *Taenia dispar*. The cirrus and vagina are dorsal to the longitudinal excretory canals, and the number of eggs produced in each proglottid is small; eight to twelve in the former, not more than ninety in the latter. They are further alike in that the uterus breaks down early before the para-uterine capsules have been formed, and in having more than one para-uterine organ.

Of the other six genera of the *Paruterinae*, five: namely, *Paruterina*, *Biuterina*, *Culcitella*, *Rhabdometra* and *Metroliasthes*, are alike flattened dorsiventrally, the proglottids are distinct at the time of maturity or earlier, the female reproductive organs are anterior to the testes and the vitellaria posterior to the ovary. The testes are small, numerous (twenty to forty), and of an inconstant number, and occupy the posterior part of the proglottid (Textfig. B). The cirrus and vagina pass between the excretory canals. (In *Paruterina angustata*, Fuhrmann, the dorsal canal has not been observed. The genital ducts, however, pass dorsal to the ventral canal.) That the eggs are very numerous is suggested by the pictures, though no one has ever counted them. The uterus is relatively large and persists until the embryos pass into the single para-uterine organ.

Thus it is seen that the genera of Fuhrmann's subfamily *Paruterinae* fall into two distinct groups in one of which is *Nematotaenia*; in the other the five genera named above. The genus *Anonchotaenia* differs somewhat from either group. While the testes are small and numerous, they are dorsally situated, and the ovary, vitellaria and uterus are arranged laterally from the genital pore in the order named. How-

ever, this difference in the position of organs seems to be brought about by the shortness of the proglottid which would not admit the anteroposterior arrangement common in the other forms. Since, therefore, *Anonchotaenia* is similar in general characters and in the aspect of the mature proglottid, and since the development of the para-uterine organ and of the uterus, which persists until the embryos have passed into the para-uterine organ, resembles that of *Paruterina* and *Biuterina* much more closely than that of any other form, I consider that *Anonchotaenia* is rightly placed in the subfamily with *Paruterina*, *Biuterina*, *Culcitella*, *Rhabdometra* and *Metroliasthes*.

For *Nematotaenia* and the species under consideration in this paper, because of the pronounced differences in the aspects of the mature proglottids, the early degeneration of the uteri and the late formation of the para-uterine capsules, of which there are more than one in each proglottid, it seems necessary to establish a new subfamily, *Cylindrotaenianae*: Cylindrical Dilepinidae having one or two dorsally placed testes, ovary and vitellaria ventral, vitellaria dorsal to ovary. Proglottids distinct at the posterior end only. The uterus breaks down early and the embryos are later enclosed in para-uterine capsules. *Taenia pulchella* Leidy would probably also belong to this subfamily.

On the other hand, notwithstanding their marked similarity in the respects noted above, *Taenia dispar* and this new worm show certain important differences. As to external characters it may be mentioned that whereas the former has its greatest diameter at the anterior end and diminishes gradually to the posterior end, the latter has its greatest diameter about midway of the strobila and narrows toward both ends.

Of greater importance is the difference in the male reproductive system. Whereas *Taenia dispar* has two symmetrically placed oval testes and the vas deferens forms a loop which passes ventrad as far as the excretory canals, this new worm has a single spherical testis situated lateral to the median line of the proglottid and a simple straight vas deferens. And whereas the cirrus sac of *Taenia dispar* is almost ten times as long as wide, that of the worm herein discussed is only two and one-half times as long as wide.

Nowhere are the differences more striking than in the development of the para-uterine organs (Figs. 5 and 12) and the aspect of the ripe proglottids (Figs. 9 and 11) for in place of the two large elaborate cone-shaped structures noted above, which are probably the most noticeable and characteristic structures of the worm, *Taenia dispar* has a varying number of small para-uterine organs in no wise characteristic; and in place of the two large, transparent, spherical para-uterine capsules found in the ripe proglottids of this form, the ripe proglottids of *Taenia dispar* have from thirteen to thirty small dark capsules scattered through the parenchyma.

From these considerations it becomes evident that this form does not belong to the genus *Nematotaenia*, which it most closely resembles of any of the genera yet established, and it is necessary to establish a new genus for its reception.

This generic description would be as follows:

Genus *Cylindrotaenia*. Scolex unarmed, without rostellum; reproductive organs single in each proglottid; pores lateral, alternating; vagina and cirrus dorsal to the excretory canals and main nerve trunk; testis one, dorsal; ovary and vitellaria ventral. Uterus breaks up into capsules surrounding the embryos which ultimately pass into two paramerine capsules.

Type species *Cylindrotaenia americana*. Characters given above. From small intestine of various Anura. Type specimens in the collections of Henry B. Ward and M. E. Jewell.

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EXPLANATION OF PLATE

<i>a</i> Apical portion of Para-uterine organ	<i>p</i> Para-uterine organ
<i>b</i> Basal portion of Para-uterine organ	<i>r</i> Receptaculum seminis uterinum
<i>c</i> Cirrus pouch	<i>s</i> Septum between proglottids
<i>e</i> Eggs	<i>t</i> Testis
<i>ec</i> Excretory canals	<i>u</i> Uterus
<i>em</i> Embryo	<i>v</i> Vagina
<i>m</i> Longitudinal muscles	<i>vd</i> Vas deferens
<i>n</i> Nerve	<i>vt</i> Vitellaria
<i>o</i> Ovary	

All figures from camera lucida tracings except 7 and 8 which are reconstructions.

Figures 1-10 *Cylindrotaenia americana*.

Fig. 1.—Scolex, $\times 37$.

Fig. 2.—Cross section of a proglottid with fully developed uterus and para-uterine organ forming, $\times 165$.

Fig. 3.—Cross section of a proglottid in the region of greatest diameter, $\times 160$.

Fig. 4.—Cross section of a proglottid at the beginning of external segmentation, $\times 160$.

Fig. 5.—Toto mount, lateral view of a somewhat later stage, $\times 175$.

Fig. 6.—Toto mount, lateral view of a proglottid near the end of the strobila, $\times 235$.

Fig. 7.—Cross section of a mature proglottid, $\times 165$.

Fig. 8.—Cross section of a somewhat later stage showing the formation of the uterus, $\times 165$.

Fig. 9.—Detached ripe proglottid, $\times 235$.

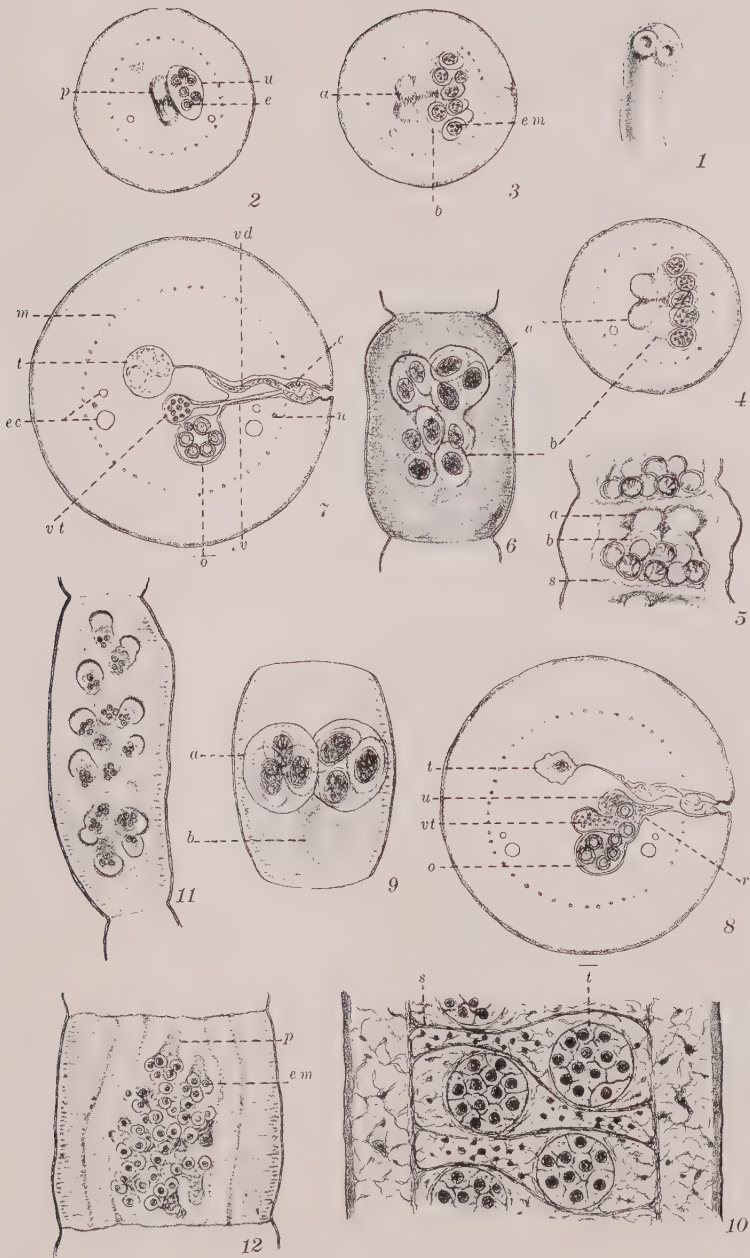
Fig. 10.—Frontal section of three proglottids in the region of the greatest development of the testes, $\times 325$.

Figs. 11 and 12.—*Taenia dispar*; from materials sent from Neuchatel, Switzerland.

Fig. 11.—Toto mount, ripe proglottid. Stage corresponding to Figure 9 in *Cylindrotaenia americana*, $\times 50$.

Fig. 12.—Toto mount, proglottid from near the end of the strobila showing para-uterine organs. Stage corresponds to Figure 5, $\times 70$.

PLATE



THE EFFECT OF TICK BITES ON MAN

D. McCaffrey

PRINCETON, B. C., CANADA

The local and constitutional effects which tick bites have on human beings is a subject which is still in the experimental stage, and I have been unable to find it discussed at any length in any of the textbooks. Osler merely mentions the fact. The only literature available is to be found in papers published in the scientific magazines.

I have had several cases which I attribute to the bites of ticks. These cases present two sets of symptoms, that is, local and constitutional. Where the local symptoms appear the tick has been forcibly removed, and the parts which it buries into its host left behind. The constitutional symptoms appear when the tick is allowed to remain on the host for some time. To illustrate the local symptoms I will describe two cases.

CASE 1.—M. M., aged 34. One night in May, 1913, on retiring, he felt an irritation along the right tibia. He rubbed the leg vigorously with the hand. Next morning the pruritus was very marked and a red spot appeared on the leg. The body of the tick was found on the floor. That day the leg began to swell and continued to do so until it was nearly twice its normal size. An abscess developed at the point where the tick's head was embedded. Hot poultices were applied for a week, then an incision made. The skin over the abscess was very tough. A creamy looking pus escaped. In about three days a hard dark colored mass came away. This was almost of a rubbery nature, and left an ulcer which extended nearly to the bone. I treated this as an ordinary ulcer for a week, but it showed no signs of healing. By that time the ulcer had hard indurated edges, giving it a "punched-out" appearance. There was a thin watery exudate coming from it. The only thing the patient complained about was the intense itching. In two months the ulcer was covered with skin. Each spring an ulcer has formed at the same place, which takes from two weeks to two months to heal. The leg itches almost constantly, at times becoming almost unbearable.

CASE 2.—Female, age 9, June, 1915. The tick was found on the mastoid bone. Her father removed it by force. Next morning the child complained of itching, and a red spot appeared. In two days the parts were much swollen and tender, with a raised spot where the head was imbedded. Applied hot poultices for four days and incised. The skin was very tough and very little pus escaped. The next day pus came from the ear as well as by the incision. On the third day after the incision was made, a dark, rubbery mass came away, leaving a "punched-out" ulcer. The ulcer has not healed as yet, Aug. 15, 1915, the pruritus being so severe that the child's hands have to be tied at night.

To illustrate the constitutional symptoms I will describe the only case I have had.

CASE 1.—D. W. Female, aged 11. May, 1915. Retired May 9, in ordinary health. When she got up the next morning her legs gave way and she fell. She walked about that day with no other symptom than falling, if she turned

or moved quickly. She could execute any movement if done slowly. The next day she could not walk and her arms were involved. Paralysis gradually extended until all the muscles were involved, leaving the child helpless. The pupils gradually dilated and lost their power of reacting to light. The tendons were at first exaggerated but later became lost. For the first four days the patient was very excitable. The muscles twitched so as to give her choreic movements; afterward she became somewhat duller but still retained most of her faculties. The involuntary muscles were the next to become affected, so that there was incontinence of the urine and feces. The breathing which was at first rapid became "choky," there being a peculiar rattling sound at each effort to breathe. She complained of a lump in her throat. If given liquids they returned by the nose. Her speech was affected so that she could hardly articulate. The tongue became swollen. The heart became very rapid, being above 120 per minute. The temperature at first rose 1 degree then dropped to 3 degrees below normal. Urine analysis negative. Sensory nerves normal. On the seventh day after symptoms appeared I removed a tick from near the crown of the head. Recovery was very rapid, so that on the third day she was able to walk up the street. In this case I had practically given up all hope of recovery. When the tick was removed I stopped all medicine and treatment. The child made a complete recovery.

I was fortunate enough to have the tick in this case identified as *Dermacentor venustus*. Whether it is *Dermacentor venustus* which causes the local effects or *Dermacentor albipictus*, which is also quite plentiful on horses in this district, I am unable to state. Princeton has an altitude of 2,000 feet and ticks are most abundant and active during the spring months and early summer; possibly they may be found higher up in the mountains at a later date. The case of "tick paralysis" I have just described is the first one of its kind that I have seen in the Princeton district. A number of cases have been reported from other parts of British Columbia, the nearest being in the Similkameen Valley some miles distant.

Dr. S. Hadwen examined the tick which was removed from the case of "tick paralysis," and determined it as *Dermacentor venustus*, a half-gorged female. He tells me that he has never seen any harmful effects from the bites of *D. albipictus* in animals, but that the local after-effects from the bites of *D. venustus* are often severe. According to Hadwen, the constitutional effects in animals following the prolonged attachment of *D. venustus* are identical to those I have just described.

SOCIETY PROCEEDINGS

THE HELMINTHOLOGICAL SOCIETY OF WASHINGTON

The twenty-eighth regular meeting of the society was held at the residence of Mr. Crawley Dec. 10, 1915, Mr. Crawley acting as host and Mr. Chambers as chairman. Dr. Cobb presented the following:

Notes on New Genera and Species of Nematodes.—Note 1.—*Antarctic Nematodes*

The free-living marine nematodes of the Mawson Antarctic Expedition represent twelve species, nine of them new (one new genus), and three species previously described in my report on the free-living nematodes of the Shackleton Expedition. This raises the number of known marine species of Antarctic free-living nematodes to thirty-four, representing eighteen genera, only three of which are new. Considering the small number and the meagerness of the Antarctic collections, these results indicate that Antarctic species of marine free-living nematodes are very numerous and belong to very widely different genera, and for the most part to genera found in warmer seas.

NOTE 2.—*Renette of Cephalobus*

I find that in some species of *Cephalobus*, and probably in the majority, the excretory or renette duct is bifurcated and passes along the lateral fields to near the posterior end of the body. This structure thus parallels that found in many species of *Rhabditis*, and as a considerable number of parasitic forms have either rhabditiform larvae, or rhabditiform free-living generations, the possibility is suggested that *Cephalobus*, or rather some species of it, may be free-living forms connected with parasites. Examination of a large number of marine free-living nemas (a contracted term proposed here for the word nematodes) has strongly impressed me with the possibility that some of these species will in the end prove to be free-living forms of parasites of fishes, marine birds, cetaceans, etc.

NOTE 3.—*A New Form of Nematode Hermaphroditism*

I have a new nematode species that is extremely interesting in the form of its hermaphroditism. The individuals have the form of females, with double sex organs, one of normal size and functioning as an ovary, the other exceedingly small, and appearing to function as a testis.

NOTE 4.—*Subdivisions of Mononchus*

I find the free-living nematode genus *Mononchus* Bastian, 1866, to be divisible into five very natural divisions, of which the first three form a group considerably differentiated from the two others which may later be raised to the rank of genera.

1. *Mononchus* typical subg.—Pharynx twice to thrice as long as wide; onchus massive, midway or farther forward, unopposed by denticules; pharyngeal walls smooth or transversely striated; males of six species known; ovaries, two, reflexed. Type species *M. truncatus* Bast. Consisting of such species as *M. brachyuris* Bütsch.; *M. parvus* de Man; *M. rex* Cobb; *M. fovearum* Duj.; *papillatus* Bast.; *M. intermedius* Cobb; *M. major* Cobb; *M. gerlachei* de Man;

M. macrostoma Bast.; *M. longicaudatus* Cobb; *M. tunbridgensis* Bast.; *M. dadayi* Micol.

2. *Prionchulus* subg. nov.—Pharynx about twice as long as wide; onchus massive, midway or farther forward, opposed by numerous denticles arranged along a longitudinal pharyngeal rib; males of one species known; ovaries, two, reflexed. Type species *Pr. muscorum* (Duj.). Consisting of such species as *Pr. muscorum* (Duj.) and *Pr. spectabilis* (Ditlevsen).

3. *Mylonchulus* subg. nov.—Pharynx goblet-shaped; onchus more or less arcuate, massive, midway or farther forward, opposed by numerous denticles arranged in transverse rows on two rasp-like areas; males unknown; ovaries, two, reflexed. Type species *My. minor* Cobb. Consisting of such species as *My. minor* Cobb and *My. obtusicaudatus* (Daday).

4. *Iotonchus* subg. nov. (gen. nov.?).—Dorsal onchus and all others usually basal, relatively small; large species with large, elongated pharynx, having three longitudinal ribs; tail rather long and slender; males of two species known; ovaries, one or two, reflexed. Type species *I. gymnolaimus* Cobb. Consisting of such species as *I. digiturus* Cobb; *I. bathybius* (Micol.); *I. studeri* (Steiner); *I. tridentatus* (de Man).

5. *Anatonchus*, subg. nov.—Onchi retrorse, midway in pharynx or sub-basal; large species with roomy elongated pharynx; tail long and usually becoming cylindroid; female organs double; males of most of the species known. Type species *A. tridentatus* (de Man). Includes *A. dolichurus* (Ditlevsen).

I have manuscript descriptions of several new mononchs from various parts of the world, all readily referable to one or another of these divisions.

NOTE 5.—Finder Slides

In an article in the Transactions of the American Microscopical Society (34:1-89) I have suggested the advisability of using co-ordinate numbers, preferably probably minus co-ordinates, dating from the upper right corner of the slide as the origin, or zero point. The slide I am exhibiting is of this kind, and presents the peculiarity that it does not have to be constantly removed and replaced when in use, thus effecting a material saving in time and energy. It consists of a series of coordinates arranged in a small holder adapted to receive and clamp the microscope slide upon and in register with the finder. Light from the microscope mirror passes through the finder and the microscope slide.

In other words, the finder slide is ruled into millimeter squares, each square containing two numbers indicating the actual distance of the square from the right-hand edge of the slide and from the top of the slide, respectively. Under the microscope the normal inversion makes these numbers appear to read from the left-hand side and from the bottom of the slide. The slide which is being studied fits over the finder and is held by two small fixed clamps. By focusing down at any point the two indicative numbers for the corresponding square may be found and noted. The slide is made by photographing a ruled and numbered sheet with such a reduction as will make the photographic squares one millimeter square.

Dr. Stiles presented a note in regard to the sanitary index of three Southern communities, A, B and C. In two of these communities, A and C, the authorities in charge had preached what they regarded as feasible, but comparatively low, standards of sanitation, including the advocacy of the unsheltered or so-called "umbrella privy." In the third community, B, the authorities had taken the position that it was not advisable to advocate something that would have to be combated subsequently, and in consequence high, even if temporarily unattainable, standards had been advocated. After the lapse of a year, the sanitary index of the three communities was again taken and compared with the index for the period of the sanitary campaign of a year before. It was

found that the sanitary index for the two communities A and C had fallen in a year from 28.1 to 24.2 for A, and from 34.6 to 29.4 for C, while the sanitary index had risen for community B from 31.5 to 45. The sanitary campaign in communities A and C was of the revival type with much attendant publicity; that of community C was of a quiet, personal nature without so much attendant publicity. It was found that the umbrella privies built in communities A and C had gone to pieces in a year.

Dr. Stiles also presented a note on memory span studies in children. Of children from homes with privy and those from homes with sewer, it was found that the memory span of the last group compared with that of the first group as 14 to 10. For thirty-six boys and sixteen girls with light infestations with hookworm, the total memory span should have tested 343.24, and did in fact test 339, showing only a very slight variation below normal. For thirty-eight children infested with *Ascaris*, the total memory span should have been 245.23, and was in fact 250, a slight variation above the normal. For sixty-seven children infested with *Giardia* (*Lamblia*), the total memory span should have been 441.6, and was in fact 444, a slight variation above the normal. For fifty-five children infested with *Entameba coli*, the total memory span should have been 367.29, and was in fact 376. It therefore appears that while children from sanitary homes show a superiority over those from insanitary homes, so far as the memory span is concerned, of 14 to 10, the presence of slight infestations with hookworm, ascarids, *Giardia* or *Entameba coli* appear to bear no appreciable relation to the memory span.

MAURICE C. HALL, *Secretary*.

The twenty-ninth regular meeting of the society was held at the residence of Dr. Stiles Jan. 28, 1916, Dr. Stiles acting as host and Dr. Pfender as chairman.

Dr. Stiles presented a note in regard to cases of spurious parasitism. A slug, said to have been passed by a patient in Baltimore, and identified by Dr. Paul Bartsch as *Limax flava*, was shown to the society. In a second case, a physician had for years been regarded as presenting a case of multiple infestation with *Cysticercus cellulosae*, this being the diagnosis of the patient and of several other physicians. A physician who had examined the patient called in Dr. Stiles, and their examination disclosed the fact that the patient was addicted to the use of drugs administered by the usual hypodermic method. The patient's failure to use a properly sterilized needle had led to the formation of the small swellings which were present over the arms, legs and the portions of the body accessible to the needle, but significantly absent over the back. These swellings constituted the supposed cysticerci. One of these swellings when excised and sectioned showed connective tissue and pus. Dr. Stiles also noted the fact that the pulp vesicles of an orange had been sent to him with a diagnosis of *Dicrocoelium lanceatum*, and predicted that next spring and summer there would be the usual amount of hairs from the strawberry sent in as supposed specimens of pinworms and hookworms. He also recalled the sending in of a specimen, said to have been vomited by a boy and supposed to be parasitic, which proved to be a placental structure, apparently from a cat, and called attention in this connection to the historical *Spiroptera hominis*, which had proved to be the entrails, eggs and encapsulated nematode parasites of fish, which had evidently been introduced into the vagina by a hysterical woman patient.

Dr. Ransom presented the following notes on spurious parasitism: There was at one time in Washington a man who was accustomed to come to the Bureau of Animal Industry with an account of a peculiar affliction consisting in his being parasitized by insects which would suddenly appear in the skin,

quickly emerge and fly away. The man appeared sane on other topics. Dr. Ransom also noted a case in which supposed flukes were sent in as having been vomited by a boy. Examination showed them to be earthworms. In another case of a similar nature the supposed parasites proved to be two earthworms and a slug.

Mr. Crawley noted a case in which blood smears were sent in with the report that they showed blood parasites. These objects proved to be a common fungous structure which occurs in feces of all sorts almost anywhere.

Dr. N. A. Cobb gave a stereopticon demonstration, discussing about thirty species of nematodes found in the sand of slow filter beds from the filtration plants of various cities, and presenting three notes thereon:

Notes on Filter-Bed Nematodes.—Note 1.—Predaceous Nematodes

The discovery of nematodes in tap water led me to an investigation of conditions at filtration plants. Nematodes were found on the walls wet with spray at the flumes where the filtered water enters the city's supply. At the end of the period of use, usually a few weeks, the sand in the beds was found to contain hundreds of millions of nemas per acre in the top 3 inches. In one case, where the tale reached about one thousand million nemas per acre, nine tenths of the specimens were of one species, the predaceous *Mononchus longicaudatus* Cobb, which feeds on other nematodes, protozoa, etc., and hitherto known only from soil. This species is cosmopolitan. Another mononch, the *Mononchus papillatus* Bastian, I have shown, feeds on the citrus-root nema, an injurious parasite of various citrus trees, and there is a possibility that the filter-bed form may be economically serviceable in destroying injurious nemas. The filter-bed form is interesting from the fact that good preparations show that the esophagus is supplied with glandular structures opening into the lumen.

Two vegetarian species of *Monhystera* were found in the filter beds feeding on microbes and other organisms, and a species belonging to a new genus has the same food habits. *Ironus ignavus* Bastian and *Ironus longicaudatus* de Man, also found in large numbers in the filter beds, show in the cells of the intestinal walls doubly refractive granules which have also been found in the lumen of the intestine, indicative of a cannibalistic food habit. *I. ignavus* has an interesting egg, with peculiar chromatic elements scattered through its cytoplasm. In both forms the renette, hitherto undiscovered, is well developed and empties near the lips. Both have esophageal (salivary?) glands emptying into the pharynx.

Tripyla monhystera de Man is a very active, rapacious, carnivorous nema feeding on other nemas and on rotifers and protozoa, and is very common in filter beds. It suffers from what appears to be a protozoan disease, the protozoan usually invading it in the region of the tail, the invasion progressing most rapidly along the lateral fields. The affected nemas lose their normal activity and show signs of disease. The infection terminates, at least at times, in the death of the host.

NOTE 2.—Syngonism and Parthenogenesis; Cryptogenesis

Among these filter-bed nemas I have quite a complete series from bisexual species, through those showing obvious syngonism with prominent development of sperm in the gone followed by egg development, to those syngones in which the sperm development is rapidly accomplished and results in relatively inconspicuous though functional sperms. So complete is this series, ending in sperm discoverable with the utmost difficulty on account of minuteness, that

the fact that in any particular case the presence of sperm was not demonstrable, as, for instance, was the case in a species of *Ironus*, could not be regarded as proving its absence. Since in syngonism there is a single primordial gonocytic cell which by division gives rise to sperm and then to eggs in the same gone within a very short time, the idea is suggested that instead of this cell division producing these various elements and then a little later uniting them in the process of fertilization, the essential processes might occur in the earlier unicellular stage and the whole affair be consummated as a more nearly simultaneous instead of a consecutive process. This theory I suggest for consideration in connection with parthenogenesis. Such a method of reproduction, if it exists, I would denominate cryptogenesis.

NOTE 3.—Revision of the Genus *Cylindrolaimus*

Careful examination of a new species of *Cylindrolaimus* from the Washington filter beds has led to a more complete characterization of *Cylindrolaimus*, and a revision of the genus, as follows:

Cylindrolaimus de Man, 1884.—Small aquatic or meadow-land species, with naked, striated cuticle; cephalic setae, four, spreading, submedian; pharynx long, narrow, cylindrical, unarmed; lips rudimentary or none; labial papillae exceedingly minute; amphids circular, depressed; esophagus cylindroid, valveless, with well-developed cylindrical cardia; intestine thick walled, granular, not tessellated; tail moderately long, usually blunt, containing three caudal glands emptying through a plain, rounded, unarmed spinneret. Ovary single, outstretched; with a small branch on the other side of the vulva. Males rare or none, and, so far as known, having two equal, arcuate spicula, with very rudimentary accessory piece; male supplementary organ one, simple, slightly elevated, opposite the spicula; *C. communis* de Man denominated type species by de Man.

Key to Species Thus Far Referred to *Cylindrolaimus*

The last species (5, 6, 7 and 9) are not *cylindrolaimi*; the genus to which each may belong is suggested in parenthesis:

- Bulb about pharynx, none; ovary one (except in No. 6); tail simply conoid; head rounded; amphids as wide as pharynx..... *f-communis* de Man 1
- Amphids half as wide as pharynx; ceph. setae half long as head is wide; oes. 20%; spin. symmetrical *-f obtusus* n. sp. 2
- Ceph. setae papilloid; oes, 14%; spinneret asymmetrical *? melancholicus* de Man 3
- Tail conoid, then cylindroid; head more or less truncate; pharynx twice long as head is wide; ceph. setae four or none; uterus and ovary simple; amphids minute or none; ovary reflexed; amph. small entering obliquely (Cylindrolaimus?) *'f tristis* Ditlevsen 4
- Ovary outstretched; no amphids, setae or spinneret (Gen. nov.?) *-f macrurus* Daday 5
- Uteri 2; ovaries reflexed; amphid a spiral (Plectus?) *'f aberrans* Micoletzky 6
- Pharynx as long as head is wide; cephalic setae 6.....(Prismatolaimus?) *-f politus* Daday 7
- Cephalic setae 4..... *-f brachystoma* Hofmänner 8
- Bulb of pharynx distinct; ovaries 2; setae none (Ethmolaimus?) *? lacustris* Hofmänner 9

C. obtusus n. sp. { $\frac{3.2}{2.0}$ $\frac{10}{2.6}$ $\frac{22}{3.3}$ $\frac{58.1}{3.5}$ $\frac{87}{2.8}$ } .6 mm. Resembles *C. communis*, from which it differs in the form of the female sexual organs, the cephalic setae, and form and size of the amphids. Ventral excretory pore opposite the middle of the pharynx. Appears to be digonic, since the small outstretched posterior branch of the sexual organ appears to function as a testis. Habitat: sand-filter beds, Washington, D. C.

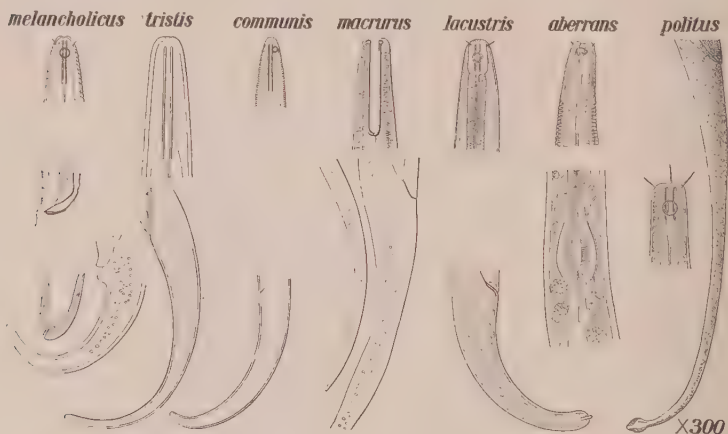


Fig. 1.—Heads and tails of species of *Cyndrolaimus* referred to in the key, reproduced from illustrations in the published descriptions of the species.

<i>melancholicus</i>	{ $\frac{1.7}{1.7}$ $\frac{?}{?}$ $\frac{14}{3.1}$ $\frac{53.71}{3.8}$ $\frac{90}{2.5}$ }	> 1.3 mm.	<i>milchlicus</i>	{ $\frac{1.7}{1.7}$ $\frac{?}{?}$ $\frac{14}{3.1}$ $\frac{53.71}{3.8}$ $\frac{90}{2.5}$ }	> 1.1 mm.
<i>communis</i>	{ $\frac{3.9}{1.8}$ $\frac{11.7}{2.5}$ $\frac{19.3}{3.1}$ $\frac{56.21}{3.7}$ $\frac{88.5}{2.3}$ }	> 64 mm.	<i>tristis</i>	{ $\frac{3}{1.1}$ $\frac{?}{?}$ $\frac{26}{?}$ $\frac{59.1217}{1.5}$ $\frac{92.6}{1.3}$ }	> 1.8 mm.
<i>macrurus</i>	{ $\frac{3.6}{2.1}$ $\frac{?}{?}$ $\frac{18.7}{3.8}$ $\frac{51.8}{4.4}$ $\frac{77}{2.5}$ }	> 1.4 mm.	<i>aberrans</i>	{ $\frac{3.9}{1.9}$ $\frac{9}{2.4}$ $\frac{15}{2.8}$ $\frac{44.11}{3.1}$ $\frac{81}{1.7}$ }	> 1.1 mm.
<i>politus</i>	{ $\frac{1.4}{1.5}$ $\frac{6.1}{2.5}$ $\frac{16}{3.4}$ $\frac{60}{3.4}$ $\frac{81}{1.8}$ }	> 1.1 mm.	<i>lacustris</i>	{ $\frac{2.8}{2.6}$ $\frac{?}{?}$ $\frac{16.6}{?}$ $\frac{50}{2.9-5}$ $\frac{64.5}{3.7}$ }	> .7 mm.

Fig. 2.—The formulae of the species referred to in the key.

Dr. Pfender presented a note in regard to a patient who thought that he had a tapeworm. Radiographs presented by Dr. Pfender showed that the symptoms which the patient referred to were due to nephrolithiasis. A nephrectomy was performed and the stones, one large one and numerous smaller ones, which had been found in the kidneys, were exhibited.

MAURICE C. HALL, *Secretary*.

REVIEWS AND NOTES

DIE TIERISCHEN PARASITEN DES MENSCHEN

1. TEIL: NATURGESCHICHTE DER TIERISCHEN PARASITEN DES MENSCHEN VON DR. MAX BRAUN. Fünfte, vermehrte und verbesserte Auflage. 560 pp. 407 text figures. Curt Kabitzsch Verlag in Würzburg. 1915. 13 mk.; geb. 15.50 mk.

The appearance of a new edition of the well-known and highly prized text by Braun is deserving of more than ordinary notice here. It is seven years since the fourth edition was published and the literature on parasitology which, especially among Protozoa, has modified and extended the world's knowledge of this important field, may fairly be said to have doubled in that short interval of time. The last (fourth) edition of Braun's work saw the addition of a clinical-therapeutic section which in this edition has been expanded to a second part, the separate appearance of which is promised at an early date. Unquestionably it was the rapid growth in materials demanding consideration which has led to the separation of the newly introduced section as an independent item; for the first part, which covers only the structure, life history, distribution and classification of the species parasitic in man, now utilizes 560 pages—or more than twice the compass of the entire work in the third edition.

The increase in size is also accompanied by marked changes in form such as to allow of more extended discussion in the same space. The type page is both larger and wider. More of the present volume has been thrown into fine type and other means of condensation have been employed freely in the effort to bring present knowledge into a reasonable compass. Unfortunately in this process the author was compelled to reduce the introduction considerably in extent, a change which every one must view with real regret for Professor Braun is an artist in presenting concisely and clearly any discussion of general principles and many generations of students have read with profit and delight his opening chapter on Parasitism in General. The general discussions with which the account of each group was introduced have also suffered somewhat in the process of condensation.

Even with all this trimming the text has grown fully twenty per cent. in volume. New material is in evidence everywhere. The new edition is in fact a real revision and not a mere reprinting with minor textual modifications. The author has added a very considerable number of new species which have been discovered since the appearance of the last edition or which since then have been found to be of significance to man. This increase runs from ten to thirty per cent. in different groups.

The plan adopted in the previous edition of grouping the important references to the literature in a section at the close of the text proper has been followed here more consistently. This list, though sharply scanned, has increased greatly in extent and now covers 110 text pages. It is notably fairer than most foreign lists in its treatment of American work and is thoroughly up to date. A few typographical errors were noted and some curious abbreviations in titles of English articles. Unfortunately the references on topics in the last 25 pages are printed in the text after the manner of earlier editions and not brought together in the bibliographic list. This detracts somewhat from the character of the work and the record is also not so good. Yet, one may say confidently that it is the best reference list available in this field.

The illustrations are frequent, good, and about one fourth of them new. Some ancient favorites that are not very accurate still occupy their historic

places. Thus the figures of *Demodex* and of the female *Ixodes ricinus* are little worthy of a place in such a work. But on the whole the work is better and more profusely illustrated than our own texts in biological science.

The section on Protozoa has perhaps been modified most of all. The system is greatly expanded and one notes that the Cnidosporidia have been exalted to the rank of a class, a conspicuous departure from the time honored division of this phylum into four classes. By the removal of the discussions concerning insect vectors (mosquitoes, biting flies, etc.) to the chapter on insects the apparent increase in size is not marked superficially, but the space gained in this way is more than filled by data on the group proper. New species, new data on morphology, life history, and biology, as well as recent experimental work, and new figures are prominent in this section.

In the chapter on Trematodes the author has introduced a systematic outline prepared by Odhner and embodying the recent important researches of that distinguished investigator on the relationships of the various groups of flukes. This system marks a distinct advance in the direction of a natural classification based on comparative anatomy and follows the line of attack formulated in Looss' epochal studies on the natural classification of the Trematodes. It is interesting to note that even in this long known and much studied group, the text lists seven species out of twenty-one that were not mentioned in the previous edition, and that the accounts of species formerly listed almost all have been radically revised in correspondence with recent discoveries concerning them. The author displays commendable conservatism in refusing to follow extreme modifications in nomenclature and yet he has not hesitated here or elsewhere in the volume to use new names when their establishment rests upon adequate study and morphological demonstration.

Among the Cestodes which furnish the fewest species to the list of human entozoa there are less changes to record. The older species have undergone little alteration though one name, *Hymenolepis lanceolata*, has been eliminated on the basis of error as indicated by Fuhrmann in 1908 in a note generally overlooked. But it will surprise even those somewhat familiar with the literature to find that among the twenty-seven species of tapeworms listed in this work seven are new within the last seven years.

No group of helminthes has undergone greater changes in recent years and is still in greater need of revision on the basis of such studies as Looss, Lühe, and Odhner have made among Trematodes, than the Nematodes. Thanks especially to Goldschmidt, our knowledge of nematode structure has been greatly advanced and full use is made of this advance in the work under review. The system is still a disconnected series of "families," based on factors very dissimilar in character and value, representing thus sometimes a small group of closely related species and in other cases a large mass of anatomically variant forms drawn together by artificial definitions. Some slight progress has been made in the solution of the difficulties by the pioneer work of Railliet and Henry which has been used by Braun. Nevertheless the "system" remains little more than a list. Under individual species Braun has added much new and important material, such as the work of Fülleborn on filarial life history, of Looss on the hookworms and other species, and of many others. A good many new species and also some new names greet the reader in this section. Fortunately figures and descriptions are now adequate in the main for an understanding of the species and for their differentiation; this which has not been true in earlier works, will do much to clear up the confusion which exists in this group.

Among the Arthropoda (mostly ectoparasitic mites and insects) one notes a fuller treatment which conforms to the now fully demonstrated rôle of these forms in the transmission of protozoal diseases. The increase is due partly, as already noted, to the transfer of such materials as in earlier editions were found

under other headings. This change has made distinctly for the unity and clarity of the work and was necessitated further by the demonstrated agency of the single form in the transmission of various parasitic organisms, e. g., the mosquito as the inoculator of several protozoa and filariae. But beyond this the arthropod section contains much new material. Especial mention should be made of the fine new figures and the carefully collated data for differential diagnosis of important species. Of course the accumulated knowledge in this part of the field is great, as exemplified by recent works devoted exclusively to it, and Braun has not attempted to include all. But as a summary this part must be recognized as a real success and a great advance over the distinctly inadequate treatment accorded this phase of the subject in earlier editions.

All in all the new edition represents a most valuable contribution to helminthological literature. It is a worthy production of the famous head of the Königsberg school of parasitologists and justly entitles him again to the congratulations and thanks of other workers in this field.

Doctor Jesus Rafael Risquez of Caracas has published an interesting study of nineteen cases of the blood fluke (*Schistosoma mansoni*) observed in eighty-six autopsies in Venezuela, fourteen of which came from the white race, none from the indian or negro, and five from half breeds; in large part the patients were born in Caracas.

The Report of the United Fruit Company's Medical Department for 1914 was reviewed in this Journal last December. The Report for 1915 confirms in essential details the conditions regarding the occurrence of human parasites on the shores of the Caribbean which were taken from the previous report and embodied in the tables of the review cited.

HIBERNATION OF MUSCA DOMESTICA

In 1913 Dr. Henry Skinner challenged the commonly accepted belief that adult house flies remained dormant throughout the Winter months. He even went so far as to say tentatively that house flies passed the Winter in the pupal stage and in no other way. Dr. Johannsen's observations at Ithaca tended to confirm Dr. Skinner's conclusion insofar as it applied to conditions in the latitude of New York State.

In January of this year an instructor in the Department, Mr. W. L. Chandler, observed several adult specimens of *Musca domestica* in the sub-basement of Roberts Hall, one of our University buildings. I have observed others in the sub-basement and around in the buildings even at this late date (April 7). These were remote from breeding places and there seems no possibility that they hibernated in the pupal stage.

WILLIAM A. RILEY

In a recent important paper Crawley has shown that when mice are fed material containing the so-called spores of *Sarcocystis muris* invasion of intestinal epithelial cells by the parasites takes place within two hours. This phenomenon is most favorably studied in the last inch or two of the small intestine. Within the cells, the parasites rapidly separate into two categories, the latter history of which shows them to be males and females.

In the male, development takes the form of a notable increase in the size of the nucleus, correlated with a loss of most if not all of the cytoplasm. Various internal changes take place within this enlarged nucleus, and eventually the chromatin becomes divided into clusters of minute granules, grouped around the periphery. These granular clusters solidify into compact balls, which elongate and produce the microgametes.

In the females, the changes are not so conspicuous. The cell becomes shorter and broader than the original spore, but there is no loss of cytoplasm nor any conspicuous enlargement of the nucleus. The nuclear chromatin remains concentrated in a large karyosome.

This sexual evolution is completed in from 9 to 18 hours, after which fertilization takes place. The further history of the zygote has not been followed.